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Social organization and ecology of Propithecus verreauxi grandidier 1867.

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Social Organization and Ecology of *Propithecus verreauxi* Grandidier

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A dissertation presented to the Board of Studies in Zoology of London University in Candidacy for the degree of Doctor of Philosophy in Primate Biology

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SUMMARY

During an eighteen-month field study of Propithecus verreauxi, quantitative data were collected on four groups of animals all of whom were habituated to the observer's presence. This permitted detailed observation of their behaviour without undue disturbance through provisioning or other direct interference. Two groups lived in the rich, semi-deciduous forests of north-west Madagascar. The other two groups ranged in a second study area, located in the arid Didierea forest in the extreme south of the island. These habitats were selected because they provided an extreme contrast with each other.

Sampling techniques were used to estimate the structure, distribution, diversity and phenology of vegetation in each study area. Meteorological data were also collected.

The effects of regional and seasonal variations in ecological parameters (including food distribution and availability, climate) on the study groups' patterns of daily activity, ranging and feeding behaviour and social organization, and on overall population density were studied and assessed.

Evidence was found to indicate the importance of both seasonal and regional variations in ecological parameters: in most respects, seasonal fluctuations in these parameters within each region were associated with greater behavioural variation than that found between the two regions at any given stage in the seasonal cycle. However, animals in the north-west lived in extensively overlapping home-ranges, while those in the south had exclusive use of almost their entire range.

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PART I:

AIMS AND HISTORICAL ASPECTS OF THE STUDY, AND A DESCRIPTION OF STUDY AREAS AND METHODS OF STUDY

PART IA: AIMS AND HISTORICAL ASPECTS OF THE STUDY

"...en somme, ce sont des animaux peu actifs,
peu remuants, peu intelligents..."

(Milne-Edwards and Grandidier, 1886)

Aims of the study

The study had three primary objectives. They are summarized below, and discussed in more detail in subsequent sub-sections.

i) Petter's surveys (1962a, 1962b, 1962c, 1965) and Jolly's field study (1966) are the only major published works, prior to 1970, on the behaviour and ecology of any prosimian species in the wild. In contrast, the literature on the Haplorhini has proliferated during the last ten years (e.g., Crook and Aldrich-Blake, 1968; DeVore, 1963, 1965; Goodall, 1963, 1965; Hall, 1962a, 1962b, 1963a, 1963b, 1965a, 1965b, 1965c; Jay, 1965; Kummer and Kurt, 1963; Struhsaker, 1967, 1969a): there was a need to assemble comparable material on prosimian species, in order to provide a broader overview of the whole spectrum of primate adaptations and, possibly, some insight into ancestral primate patterns of behaviour (see Charles-Dominique and Martin, 1970 for a further discussion of the latter point).

ii) The discovery of extensive regional variations in social organization has already demonstrated the limited applicability of the concept of "species-specific" behaviour to several Old World primate species (Papio anubis - Rowell, 1966; Hall and DeVore, 1965; Presbytis entellus - Jay, 1965; Ripley, 1967a; Yoshiba, 1968; Sugiyama, 1967; Cercopithecus aethiops - Struhsaker, 1967; Gartlan and Brain, 1968). No such investigation of any prosimian species has been made, and one aim of this project was to study the flexibility of social organization in a prosimian species by comparing groups from populations living in widely contrasting habitats.

iii) Attempts have been made to produce a classification of primate social organizations, and to correlate variations in social organization with ecology (DeVore, 1963; Hall, 1965c; Crook and Gartlan, 1966; Crook, 1970; Eisenberg et al., 1972). These efforts have not been altogether successful, partly through a lack of detailed information on the behaviour and ecology of many primate species. Since there are now extensive data on Old World and New World leaf-eating monkeys (Ripley, 1970; Clutton Brock, in press; Yoshiba, 1968; Bernstein, 1968; Poirier, 1969; Manley, in press; Marler, 1969; Chivers, 1969; Richard, 1970), it seemed useful to provide comparative material on a prosimian species a high percentage of whose diet consisted of leaves and shoots. The study's comparative approach (see ii) was also used in this context, in an effort to understand more clearly the processes by which ecology may influence social organization.

Propithecus verreauxi was the most suitable species for study in a project with these aims, because

i) it is widely distributed through a great diversity of habitats; (P. verreauxi is the only diurnal species found in both the arid Didierea forest of the south and the rich semi-deciduous forests of the north-west.)

ii) its diet was reported to contain a high percentage of leaves and shoots (Petter, 1962a; Jolly, 1966);

iii) previous studies (Petter, 1962a; Jolly, 1966) contributed valuable comparative material to an overall understanding of the species.

Previous studies of Propithecus verreauxi

"Il y a encor vne espece de gnenuche blanche, qui a vn chaperon tanne, et qui se tient le plus souuent sur les pieds de derrier..." Sieur Etienne de Flacourt's description of P. verreauxi in 1658 was the first written account of the species. He subsequently died of gout, and no more was heard of the species until Bennett gave it the generic name Propithecus

in 1832. P. verreauxi was scientifically named as a species by A. Grandidier in 1867, and the four sub-species, P. v. verreauxi, P. v. coronatus, P. v. deckeni, and P. v. coquereli, were named between 1867 and 1931.

The nineteenth century was a period mainly of collection, description and anatomical studies, which reached its zenith in Milne-Edwards' and Grandidier's detailed account of all the lemurs in the "Histoire naturelle des mammiferes: Histoire physique, naturelle, et politique de Madagascar" (1890-1896). These studies have recently been surveyed by Hill (1953).

The first reference to lemur behaviour was made by Shaw (1879) although he made no specific mention of Propithecus. Kaudern (1915) attempted to trace the evolution of the species and sub-species of Propithecus through their anatomical characteristics; collecting material for this work, he noted that P. v. coquereli in the wild lived in groups of 3 - 12. From animals shot on expeditions, he estimated that gestation took 4 - 5 months, and that mating occurred at the end of the rainy season. Elliot (1912) noted that "during the heat of the day, animals sleep in some secluded place among the foliage and are active in early mornings and evenings..." Grandidier and Petit (1932) recorded that Propithecus lived in groups of 6 - 8, rested in the heat of the day, and had only one young at a time. Hill (1953) cites Webb, who travelled in Madagascar in the 1940's, with reference to the mating season: "...males sometimes fight, generally seasonally, and hence probably the result of rut; evidence is seen in frequency of torn ears and patches of missing fur..."

The most extensive description of Propithecus' behaviour prior to Petter's work was given by Rand (1935). He recorded P. v. deckeni living in groups of up to 9, and described their locomotion: "...when the animals were travelling slowly, they sometimes took a few waddling steps. At no time did they travel on all fours..."

These data collected on the behaviour of P. verreauxi up until 1962 were very limited but have been shown by further research to have been substantially accurate. Petter (1962a) made the first major survey of lemur ecology and behaviour, including an account of P. v. coquereli. This provided a most valuable basis for Jolly's (1966) subsequent, more detailed study of P. v. verreauxi and for my own study of both sub-species. The work of both Petter and Jolly are referred to and discussed in the context of specific questions throughout this thesis, so no further description of it is given here.

Although studies of various aspects of prosimian behaviour in captivity have been made (Andrew, 1963a, 1963b; Buettner-Janusch and Andrew, 1962; Evans and Goy, 1968; Bishop, 1962; Jolly, 1964a, 1964b; Petter-Rousseaux, 1962, 1964) none of them related specifically to P. verreauxi. This is probably due to the difficulty found in keeping animals alive in captivity: at present, there is only one breeding colony in existence outside Madagascar.

Intra-specific variation in the social organization of other species

In a discussion of primate social organization, Hall (1965) postulated that there might be important intra-specific variation in the social organization of widely distributed species, although at that time there was little evidence to support this thesis. Subsequent studies (see P. 2) have endorsed Hall's hypothesis: the observations on Cercopithecus aethiops summarized below illustrate the nature of the variation that may be found within some Old World primate species.

A study of the ecology and behaviour of C. aethiops was carried out on Lolui Island, "an ecologically rich area", situated in Lake Victoria (Hall and Gartlan, 1965). The vegetation on this island was characterized by coastal forest, with an encroachment of thicket vegetation inland into the grassland. This provided "ideal C. aethiops country" (Gartlan and Brain,

1968). Maximum group size was estimated to be about 21, but a typical group consisted of about 11 animals; this might include two adult males, four adult females and five juveniles and infants. Groups ranged in a fairly small, but well-defined and strongly defended territory.

A parallel, but briefer study was also carried out at Chobi, on the north bank of the Nile. The relic forest of this study area was subject to elephant damage, and to grazing pressures exerted by numerous game animals. Gartlan and Brain (1968) called it "an impoverished and deteriorating habitat." At Chobi, each group of C. aethiops needed much more space than at Lolui, but despite the increase in home-range size animals appeared to be "noticeably unhealthy." Chobi groups were often widely dispersed within their home-ranges, and two features are suggested to have been a consequence of this: firstly, a signal system not seen at Lolui in this context had apparently developed, "...adult animals starting to walk through the grass often moved the first few yards with their tails held vertically, an efficient means of locating their position for other members of the group..." A second mechanism for increasing group cohesion may have been the more intense mother-infant bond: "...the 'jealous reaction' of infants was more commonly seen..." (Gartlan and Brain, 1968).

In summary, while C. aethiops on Lolui Island lived in cohesive groups in small, well-defended territories, at Chobi much greater group dispersion was associated with large home-ranges and certain behavioural features that seemed to have emerged to counter the disintegrative effects on group structure of wide dispersion.

Referring to the forest-dwelling Cercopithecus mitis for comparative material, Gartlan and Brain (1968) noted that "because of the more stringent environmental requirements of C. mitis, if environmental factors are accepted as causal in social variability, one is less likely to find variable social systems within this species..." However, studies of

Presbytis entellus in India (Jay, 1965; Suyiyama, 1964, 1965; Sugiyama et al., 1965; Yoshiba, 1968) have shown that extensive variation can also be present in forest-living monkeys. This study set out to discover if such variation is also present in forest-living prosimians.

The classification of primate societies

Among the primates, social organization may vary enormously from species to species and attempts have been made to systematize this inter-specific variation (P. 3). Classifications have been based on the premise that social organizations are adapted to, and vary in accordance with, ecology.

The first attempts to provide a functional interpretation of inter-specific variation in social organization were made by DeVore (1963) and Hall (1965): the social system of savannah-living baboons was related to selective pressures of their environment. It was postulated that, as a result of predation pressures and the distribution of food resources, they were organized into large, multi-male groups living in large home-ranges, with pronounced sexual dimorphism and male dominance hierarchies. DeVore (1963) argued that "...the increased predation pressure on the ground leads to increased morphological specialization in the male with accompanying changes in the behaviour of individuals and the social organization of the troop..." Thus, dominance was held to be associated with a trend towards sexual dimorphism, which equipped adult males for effective fighting and, specifically, for defence of the group.

Hall (1965) placed greater emphasis on food distribution as a determinative factor, arguing that a socionomic sex ratio approaching parity was more important for group defence than large group size as such and that "....While there can be no doubt of the effectiveness of the combined aggressive-defensive potential of several fully-grown male baboons...it would seem that the determinants of regional variations in group size are primarily to

be found in food density..." He also pointed out that the social organization of the patas monkey was not in accordance with the general hypothesis.

Crook and Gartlan (1966) put forward the first comprehensive theory of the relationship between ecology and social organization, proposing five ecological/behavioural "Grades":

a) Grade I comprised the forest-living, nocturnal primates. Their diet consisted mainly of insects, and they had a generally solitary form of social organization.

b) Grades II and III contained diurnal, forest-living, frugivorous or folivorous species living in cohesive groups. Grade II contained species grouped into "small family parties" and

c) Grade III contained species grouped into small to occasionally large parties, that might contain more than one adult male. Groups from both these grades often exhibited marked territorial behaviour.

d) Habitat types included in Grades IV and V were forest fringe, tree savannah, and grassland or arid savannah, with marked seasonality. Characteristics of Grade IV species were medium to large groups containing several males exhibiting marked sexual dimorphism, living in home-ranges with either mutual avoidance or combat between groups.

e) In contrast, Grade V species lived in medium to large groups but frequently fragmented and the basic social unit was the one male group.

The most recent review of primate social organizations (Eisenberg et al., 1972) grouped social systems on behavioural criteria alone; ecological correlates were not integrated into the classification, but the adaptive functions of different types of social organization were discussed. Five types were described:

1. solitary species
2. parental family

3. minimal adult male tolerance (uni-male troop)

4. intermediate male tolerance (age-graded-male troop)

5. highest male tolerance (multi-male troop)

The first two categories correspond closely to Crook and Gartlan's Grades I and II, although Eisenberg et al. emphasize the reservations with which the term "solitary" should be applied to a social system: "...solitary species, whether primates, carnivores, or rodents, have a social life, and indirect communication is maintained among adults that have neighbouring or overlapping home-ranges..." This is borne out by recent field studies (Charles-Dominique, 1971; Charles-Dominique and Hladik, 1971; Charles-Dominique, 1972; Martin, 1972).

The third category, the uni-male troop, is distinguished from the parental family by "increased representation of sex and age classes in the troop." In order to form such groups, it is argued, "...adult females must be tolerant of one another and have affiliation mechanisms to promote cohesiveness..." Further, male herding behaviour may contribute significantly to cohesiveness.

The fourth category, the age-graded-male group, introduces a new term into the classification of primate social organizations. This system is intermediate between the uni-male and multi-male structures, and defined as follows: "Although several males of varying ages co-exist in such troops, there are proportionately fewer males in these troops than there are in true multi-male troops (whose sex ratio may approach 1:1). The linear male dominance order is based on the age of the males, with no definable subunit of several males in the oldest age bracket. The lack or absence of fully adult males of equivalent age is the characteristic that defines an age-graded male troop..." It is contended that although the age-graded male troop may be considered a phylogenetic step towards the true multi-male system, a "...fundamental tendency toward polygyny and the possibility of the troop's

splitting and returning to a uni-male condition remain. Thus, the age-graded male-troop is a variation on the uni-male theme."

The fifth category, the multi-male troop, is defined by the presence in one troop of several adult males of an equivalent age.

General problems arising from current classificatory systems

The classifications proposed by Crook and Gartlan (1966) and Eisenberg et al. (1972) pose a number of problems:

i) Both classifications lump into single categories highly diverse social organizations. For example, Crook and Gartlan's Grade II contains Propithecus sp., Lemur sp. and Hylobates sp. Sussman censused 17 groups of L. fulvus rufus ranging from 4 to 17 in size, and containing at least two adult males in all cases (in press); extensive surveys of L. catta (Jolly, 1966; Klopfer and Jolly, 1970; Sussman, in press) have shown that this species lives in multi-male groups ranging from 12 to 24 individuals in size. Propithecus verreauxi has been recorded living in groups of 2 to 13, these groups often containing more than one male (Jolly, 1966; Sussman, pers. comm.). In contrast, Ellefson (1968) reported that in Hylobates lar social units were composed uniquely of adult pairs with their sub-adult offspring. Again, in Grade IV, the cohesive group structuring of Cercopithecus aethiops (Struhsaker, 1967; Gartlan and Brain, 1968) is classified with the highly flexible, fragmented grouping system of Pan satyrus (Van Lawick Goodall, 1965). Grade V lumps the discrete one-male-group system of the patas monkey (Hall, 1965), with that of Papio hamadryas, and Theropithecus gelada, where one-male groups form into large herds depending on the availability of food and sleeping sites (Kummer and Kurt, 1963; Crook, 1966).

In addition to lumping E. patas, T. gelada and P. hamadryas into a

"minimal adult male tolerance" category, Eisenberg et al. also included Alouatta palliata. This was done primarily on the basis of a census carried out on Barro Colorado Island by Collias and Southwick in 1951. At that time, only 6 out of 29 groups had two males, and none had three or more males. In summary, they found group size halved, sex-ratio halved, and a considerable decrease in the proportion of young in each group in comparison with Carpenter's results in the 1930's (1934). Carpenter gave as the "central grouping tendency" at that time 3 adult males, 7 adult females, 4 juveniles and 3 infants, and Chivers (1969) counted twelve groups all of which contained at least 2 adult males, with a mean of 3.3 adult males per group. No evidence was put forward to suggest that these groups were composed of small, one-male units. Thus, the bulk of the evidence suggests that A. palliata's social organization is quite different from that of the Old World terrestrial Cercopithecidae living in one-male groups. Collias and Southwick (1952) noted a massive drop in population size, possibly due to an outbreak of yellow fever, and it seems likely that the "one-male groups" they found were a temporary phenomenon resulting from male mortality rather than a population norm.

Eisenberg et al.'s fourth category, "Intermediate male tolerance", lumps together the social organization of Gorilla gorilla with that of Miopithecus talapoin. The gorilla is largely terrestrial, and is found in groups of 2 - 30 with a home range of 10 - 15 square miles (Schaller, 1963), while the talapoin monkey lives in cohesive troops of 85 - 158 members in a home-range of 4 - 5 squ re miles, and leaves the trees only when using rivers as an aquatic escape route (Gautier-Hion, 1966).

Finally, in the "highest male tolerance" category Pan satyrus is grouped with Papio cynocephalus, Papio ursinus, Papio anubis and Cercopithecus aethiops. The validity of such a grouping has already been questioned with respect to Crook and Gartlan's Grade IV.

ii) Although Eisenberg et al.'s newly proposed category, the 'age-graded-male troop,' may be usefully applied to some species, such as Presbytis senex (Manley, pers. comm.) (althouth Eisenberg et al. in fact allot this species to their 'uni-male troop' category), there are problems over its definition. It is stated that "The linear male dominance order is based on the age of the males, with no definable subunit of several males in the oldest age bracket. The lack or absence of fully adult males of equivalent age is the characteristic that defines an age-graded-male troop..." but nowhere are the criteria discussed by which the age gradations of fully adult males in the wild are judged. Thus the argument comes close to circularity: where males are found in a linear dominance hierarchy, age gradations are bound to be present, and vice versa. Clutton-Brock (in press) has also pointed out the difference between age-graded-male troops and multi-male troops may simply be a function of group size, and more apparent than real: where ecological conditions lead to groups comprised of a few animals, the absence of an oligarchy of adult males may reflect small group size rather than mutual intolerance of adult males of equivalent age.

I do not consider the evidence sufficient to include Alouatta palliata, Saimiri sciureus, Miopithecus talapoin, Cercopithecus aethiops and Gorilla gorilla in this 'age-graded-male troop' category. Field studies on these species have consistently found more than one adult male in each group, and no data were produced to indicate that these males were not of 'roughly equivalent age' (see Carpenter, 1934; Chivers, 1969; Thorington, 1967; Baldwin, 1968; Gautier-Hion, 1966; Struhsaker, 1967; Schaller, 1963). Thus, while it may be reasonable to distinguish the social systems of these species from those of the baboons, there seems little justification a) for grouping these species together and b) for calling the 'age-graded-male troop' the fundamental unit of their social organization.

iii) Crook and Gartlan (1966) and Eisenberg et al. (1972) see the main determinants of social organization as being food availability and dispersion, predation pressures and the type and availability of sleeping sites. This idea is further developed by Crook (1970). However, Struhsaker (1969b) has stressed the importance of the interrelations of ecology and phylogeny: "...in some cases, the immediate ecological variables may limit the expression or development of social structure and, with other species and circumstances, variables of phylogeny may be the limiting parameter..." He suggested that the one-male group typical of most Cercopithecus occurs regardless of gross ecological differences and that it is phylogenetically determined.

Rowell and Chalmers (1970) carried this argument further: "We would suggest, therefore, that among Ugandan monkey species with which we are familiar, environment does not appear to correlate with patterns of social organization, but that taxonomic position, and possibly reproductive patterns, would have better predictive value. This, we think, carried the implication that in this area there is no strong selection pressure for specific patterns of social organization in each ecological niche..."

However, phylogeny should not be considered to be the whole answer. For example, the social organization of Colobus badius differs considerably from the congeneric C. guereza (Clutton-Brock, pers. comm.), while that of Callicebus molloch shows similarity to Hylobates lar, a species classified in a different suborder (Mason, 1968; Ellefson, 1968). Goss-Custard et al. (1972) note that "...phylogenetic characteristics must in the long-term themselves have been moulded by ecological factors..."

Thus, while a phylogenetic approach cannot contribute to our understanding of the way in which a given social organization functions, it may give insight into evolutionary associations between social systems and, as such, it should be considered in classifications.

iv) A further consideration not taken into account by classifications to date is discussed in detail by Goss-Custard et al. (1972). This is the bearing that social structure may have on the reproductive success of individuals, rather than simply on the survival of individuals or groups. It is argued that "...females are limited in their capacity to increase the number of births, but males are capable of siring several litters at once. The resultant sexual selection may under certain ecological conditions give rise to a harem group structure, and also to territoriality between groups or individuals. Rearing of young may be facilitated by the formation of long-term groups in which the young can benefit from the accumulated experience of the adults. Males may increase the chances of survival of their females and young by ensuring for them an adequate supply of resources, and perhaps by minimising the risk of predation..." A number of contrasting primate social systems are then discussed, but not classified, in the light of these suggestions: Cercopithecus mitis, for example, is used to illustrate the territorial one-male group, and hence a social system which both enhances adult survival and also permits a male to father several offspring at once and a female to increase the success with which she rears her young.

If it is accepted that factors of this nature may influence social organization, then straightforward interpretations of group size as a function of ecological pressures alone are likely to be spurious.

v) The apparently contradictory evidence cited above (Pp.10-12) points up a further oversimplification in current theories linking ecology to social organization: the habitats are classified by blanket terms such as "forest," "woodland savannah," or "arid savannah," thereby ignoring variation in, for example, the structure, composition and seasonality found in different forests. Again, species are customarily referred to as "folivores," "frugivores," or "insectivores"; yet the diet of the howler monkey, a

reputed folivore par excellence, may at a given moment consist of 95% figs (Altmann, 1959), and that of some of the supposedly "insectivorous" lorisids of a high proportion of vegetable material (Charles-Dominique, 1971).

If ecological correlates of social organization are to be found, they must be sought at a more detailed level of analysis of both ecology and social organization than has been attempted in the past. Clutton-Brock's study (in press) exemplifies this more detailed approach: the correlations he demonstrates are based on a two year quantitative analysis of the diet and ranging patterns of just one group of Colobus badius and of the composition and structuring of the forest constituting their habitat. Yet even at this level of detail the results were far from being conclusive (Clutton-Brock, in press): group size, structuring, and composition, and inter-group relations must, together with the factors investigated by Clutton-Brock, form an adaptive complex. Thus direct, consistent correlations between a single environmental parameter and any single aspect of social organization, such as group size, are unlikely to be found.

Extending this theme it should be stressed that if social organization, in its most comprehensive sense, is closely related to ecology, it cannot necessarily be assumed that two species with broadly similar diet and habitat will have a similar social organization. First, minor shifts in dietary composition and thus probably in the availability, size and dispersion of food sources may have far-reaching effects on certain aspects of social organization. Since Gause's Principle of Competitive Exclusion is still upheld in ecological theory (Boughey, 1971), primates living in the same habitat cannot, by definition, occupy the same niche under stable conditions; thus, theoretically, the social systems of different species in the same habitat should show differences, reflecting the differences between the niches occupied. Secondly, as noted above (P. 13), the adaptive response of two species to a given set of environmental parameters may,

when mediated each by its own phylogenetic heritage, be radically different. It is possible, for example, that the contrasting social organizations of E. patas and P. ursinus, both savannah-living forms and apparently well-adapted to their habitat, reflect a difference in phylogenetic heritage: the "problems" posed by the environment can be "solved" by species in more than one way.

Functional interpretations of the inter-specific variation found in primate social organization

It is clear that there are problems involved in the rationale underlying current classifications: that social organization and gross categories of ecology are related on a simple one-to-one basis. The resulting classifications are themselves unsatisfactory in that they lump together species that appear to have little in common. However, it is worth considering separately the plausibility of the adaptive functions attributed to different types of social organization in these classifications.

Crook and Gartlan (1966) relate the "solitary" habits of the nocturnal primates to their insectivorous diet: insects provide a dispersed, mobile food source to which their predators respond with a dispersed form of social organization. This pattern is also found in other, non-primate insectivorous species such as the pangolin (Pages, pers. comm.). However, as Crook and Gartlan note, two species of Malagasy lemuriforms are nocturnal, "solitary," and folivorous; these are Lepilemur mustelinus (Charles-Dominique and Hladik, 1971) and Avahi laniger (Petter, 1962a). Although further information is necessary on both the diet and social organization of these species, the current evidence indicates that they are real exceptions to the proposed correlation that "solitary" equals "insectivorous." Thorington (1968) recorded that Saimiri sciureus, a diurnal, group-living species, spent a large proportion of foraging time looking for insects. Thus two

separate instances suggest that while the correlation generally holds good, it is not an invariable rule and other factors may be operative. Eisenberg et al. (1972) suggest that solitary habits may result from animals being nocturnal, "since the coordination of groups would be difficult." This seems unlikely, since there is evidence that diurnal group-living species coordinate their movements by vocalizations (Gautier-Hion, 1970) in rain forests where visibility is restricted by the dense foliage; presumably nocturnal primates could equally well maintain groups by auditory rather than visual signals if this form of social organization were adaptive.

Crook and Gartlan (1966) relate the change from nocturnal solitary habits to diurnal social habits to "...a change from a diet requiring individual hunting to food sources often locally distributed and at which social responses allow congregation for exploitation in common..." This seems a reasonable premise, but they then go on to relate the small size of social units in many forest frugivores to "...limiting conditions of food supply occasioned by the relatively stable conditions of tropical rain forest..." Crook (1970) expanded this idea, arguing that the stable food supply in many forests is likely to produce a population equilibrium just below the "ceiling" imposed by the availability of food, and that selection may consequently favour "adaptations permitting increased environmental carrying capacity rather than a seasonal maximum recruitment common in less stable regions." In effect, these adaptations would reduce intra- and inter-specific competition and increase the means of protection from predators. Crook (1970) postulated that the small, territorial groups of many frugivores represent an adaptation of this kind, and that such a form of social organization would reduce both inter- and intra-group competition.

While this theory seems to be applicable to species such as Hylobates lar, its general validity can be questioned on two grounds. First, there is mounting evidence that "gross, overall seasonal fluctuations" in food supply do occur in tropical rain forests (Richards, 1966; Ellefson, 1968; Medway, 1970). Secondly, studies of the frugivorous Pan satyrus (Suzuki, 1969), Ateles geoffroyi (Eisenberg and Kuehn, 1966), and Cercopithecus mitis (Aldrich-Blake, 1970) suggest that their social organization is closer to the model proposed by Eisenberg et al. (1972) for frugivores. They argued that since frugivores needed to find ripening fruit trees within their home-range each day, "...the best feeding strategy involves breaking up the troop into small, independently foraging units that spread out to locate fruit trees within their home-range and then 'announce' the location of feeding spots..." However, this model is clearly not applicable to H. lar.

Crook and Gartlan (1966) did not attribute a particular function to patterns of dispersion in folivores, but Eisenberg et al. stated that "...although primary folivores such as Colobus guereza and Presbytis senex eat considerable quantities of fruits, their feeding strategy is not predicated on a daily need of finding ripening fruit trees within their home-range. Small cohesive, uni-male social units are permitted within this strategy..." However, recent studies of Colobus badius and C. guereza (Clutton-Brock, in press; Struhsaker, pers. comm.; Oates, pers. comm.) have shown considerable dietary differences between these two, closely related and reputed "leaf-eaters"; while C. guereza lives in small groups containing fewer than 14 individuals, C. badius may live in groups containing up to 80 animals. It should also be noted that H. lar, a "frugivore," lives in "...small cohesive, uni-male social units..." with a strongly defended territory.

Crook and Gartlan (1966) attribute the social organization of savannah-

living primates to "...the interaction of selection pressures from food shortage, predation and habitat topography..." They postulate specifically that "open country conditions of food supply and predation favour increase in group size..." Crook (1970) develops this idea that the different forms of social organization in the savannah represent adaptive responses to differences in "...the pattern of food availability in terms of food item dispersion and seasonal variation in abundance, the incidence of predators and the type of sleeping sites available in the area..." While the argument is plausible concerning food, there is little evidence to suggest that predation is an important factor in selection for increased group size: Hall (1965) suggested that socionomic sex ratio rather than absolute group size was critical for defending a group from predators. Goss-Custard et al. (1972) pointed out that "one would expect some correlation between this type (multi-male troops) of social structure and the kind and severity of predation. The presence of multi-male troops in open areas largely free of predators...does not accord with this expectation." During a five year study of three adjacent baboon troops in Uganda, Rowell (1969) found no evidence that predation contributed to overall mortality. However, the absence of predation cannot be taken as being indicative of an absence of predation pressure: it could be a measure of the success of the social structure in minimizing effective predation. It is also possible that there has been a real reduction in levels of predation recently, due to human interference.

Thus, while functional interpretations of social organization offered by Crook and Gartlan (1966) and by Eisenberg et al. (1972) fit the evidence in some instances, none provide a consistent basis for predicting social system according to ecology. It is clear that a detailed understanding of many more parameters, relating both to ecology and to the social organization of the species under consideration, is necessary before

sound interpretations of predictive value can be made.

Methodology

Some system of data quantification was vital during the field study in order to assess more accurately the nature and significance of inter-specific variation in Propithecus. While qualitative assessments undoubtedly constitute an important aspect of any study, they can provide only relatively crude measures and their significance cannot be tested statistically. Also, it was probable that distinctions and patterns would emerge from quantified data that would go unnoticed by an observer in the field.

Quantification and the problems involved. Three basic approaches to the problem of quantification, each with its inherent drawbacks, have been adopted in field studies in the past. However, all three assume in common that a continuous record is both impossible to maintain and superfluous, in the field, and the behaviour of subjects is sampled at fixed intervals (see P. 38).

a) Latitudinal sampling. Using this method, the behaviour of all animals visible to the observer is recorded at fixed intervals (see Chalmers, 1968; Crook and Aldrich-Blake, 1968; Clutton-Brock, in press). This technique maximizes the sample size at any given moment, and gives a considerable degree of statistical independence to the data collected. However, information collected in this way is liable to be distorted by observer bias: undue weight will be given to more easily visible activities.

b) Longitudinal sampling. A longitudinal sample involves repeated observations at set intervals on one individual. This method provides information on the sequence of activities performed by an animal and, as long as the observer starts and ends the observation bout, bias due to differential visibility is minimal. However, the number of independent observations that can be made in any one period of observation is limited,

and the method may be impractical if animals are difficult to identify individually or to follow for prolonged periods. A few studies have employed this technique successfully, though (e.g., Smith, 1968; Richard, 1970).

c) Predominant group activity. Here, the observer records the "major activity" of the group, i.e., the activity which the majority of the group visible is performing (see Chivers, 1969). This method treats the group as one individual, and assumes a high degree of synchrony of activity between the members of the group. As with a), data are liable to be biased towards the more easily observed activities, and can provide no measure of the amount of time any one individual spends performing a given activity.

Methods used. Since almost all the animals studied could be individually recognized and were rarely more, and frequently less, than 10m. away from me, most information was collected using the longitudinal sampling technique described in b). By this means it was possible to build up a detailed profile of each member of each group, enabling subsequent analysis to be made of variations in behavioural patterns between the different age/sex classes within each area as well as between each.

A brief latitudinal sample, as described in a), was made in the course of the study in order to investigate the degree of synchrony of activity between group members.

Approach taken in presentation of results. The study investigated aspects of the ecology and social organization of P. verreauxi in two contrasting habitat types. In Part IB, a description of the two study areas and a more detailed account of methodology is given. In Part II, observations on the ecology and social structure of the study groups in each area are described and considered together in the following categories:

1) Group composition and population dynamics. This section provides an overview of the nature of the social organization and grouping patterns of the species.

2) Description and analysis of the structure and composition of the forest in each study area. This parallels the approach taken in 1), but in this instance describes the nature of the habitat in which the four study groups were found.

3) The following three sections focus on a more detailed analysis of the use made of the habitat by the groups studied. Results are divided into three parts: home-range size and utilization, ranging behaviour, and diet and feeding behaviour.

4) In Section VI, the emphasis is shifted from a consideration of the relationship of the animals to their organic environment to a consideration of patterns of activity in relation to climatic factors.

5) In Sections 7 and 8, the social structure and mating season are considered separately and then discussed together as complementary parts of a total social system.

In Part III, an attempt is made to integrate the results given in Part II and to provide some insight into the "how" and the "why" of P. verreauxi's social organization.

SUMMARY

1) The study had three primary objectives:

a) to assemble material on a prosimian species in detail comparable to that available on many species of Old World primates;

b) to study the flexibility of social organization in a prosimian species, by comparing samples from populations living in widely contrasting habitats;

c) to investigate the ecological parameters that may influence social organization, by the use of a detailed, quantitative approach.

2) Propithecus verreauxi was selected for study because it is widely distributed in many different habitats in Madagascar. Since its diet was reported to contain a high percentage of leaves and shoots, comparisons could be made between this species and the well-studied "leaf-eaters" of the Old and New World. Comparative material was available from two previous studies, which contributed to an overall understanding of the species.

3) Although the morphology of the lemuriforms has been widely studied, no intensive study of their behaviour was made prior to the 1960's. Since then, detailed accounts of several species have been published by Petter and Jolly.

4) Recent studies, such as that of Cercopithecus aethiops, have demonstrated the considerable intra-specific variation in behaviour to be found in some species. This variation appears to be related to ecological variations.

5) Social organization in the primates varies widely from species to species, and attempts have been made to systematize this inter-specific variation and to relate it to ecological variation. Crook and Gartlan (1966) proposed five ecological/behavioural "Grades" into which they classified known primate social systems. Eisenberg et al. (1972) divided primate social systems into five categories based on behaviour alone. These included a conceptually new category, the "age-graded-male troop."

6) A number of problems arise from these classifications. The classifications of both Crook and Gartlan (1966) and Eisenberg et al. (1972) lump into single categories highly diverse social organizations. Eisenberg et al.'s "age-graded-male troop" is ill-defined, and there appear to be no grounds for the allocation to it of a number of the species they list.

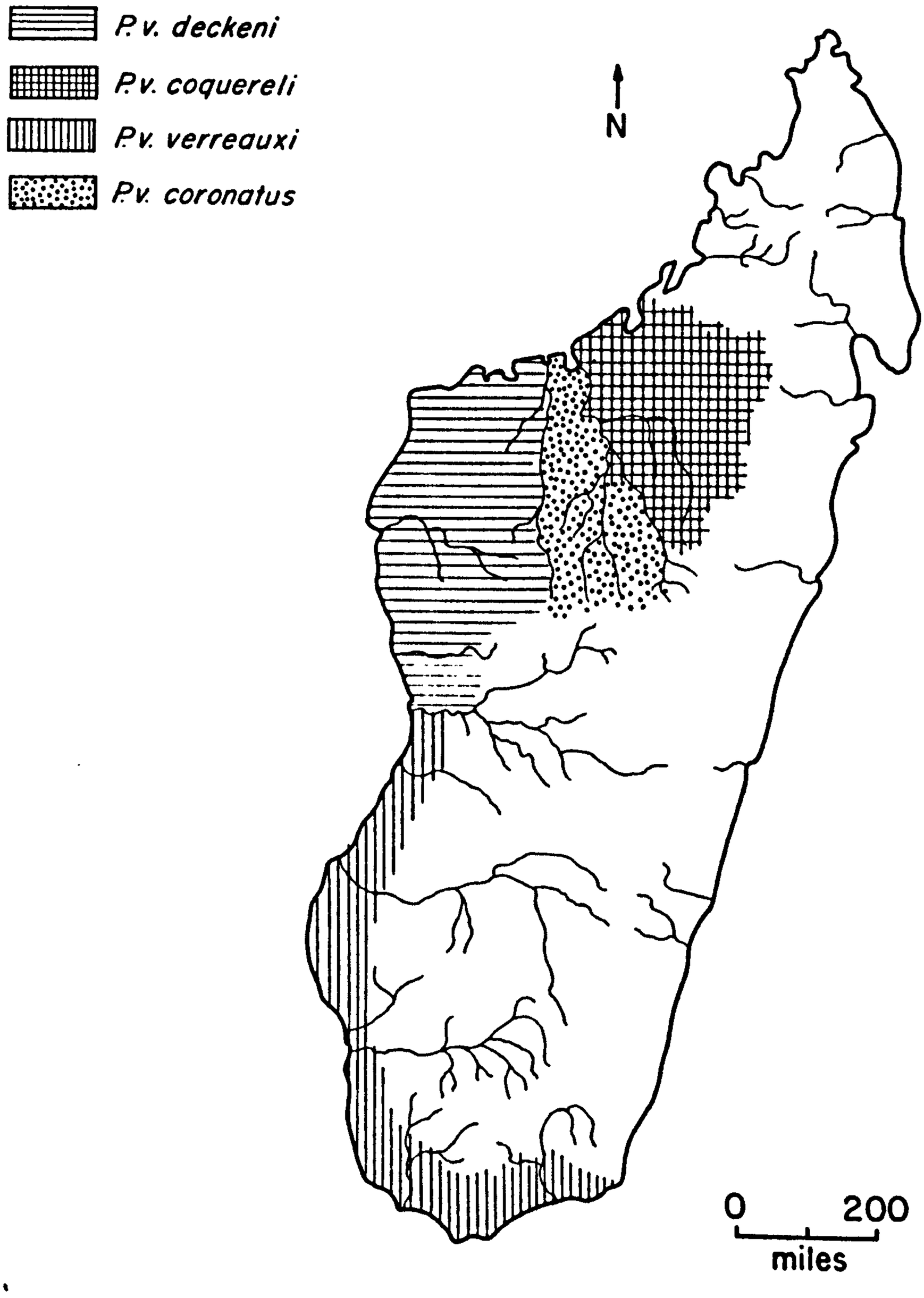
The classifications do not consider the possible mediating influence that phylogenetic heritage may have on the social organization of different species, although clearly phylogeny should not be thought of as the only causal factor involved. Another possibility ignored by current classifications is that social systems may be adapted not only to promote the survival of individuals or groups in a given habitat, but also to maximize the reproductive success of group members. Finally, it is suggested that the terms in which the ecology and social organization of primate species have been described are too gross. Both should be seen as a complex of inter-related factors, and consistent correlations should not be expected between general "habitat types" and any one aspect of social organization.

7) A brief review of the adaptive functions attributed to different types of social organization reveals that much of the evidence appears to contradict the postulated "rules." Here again, the problem seems to be a lack of sufficiently detailed information on aspects of ecology such as the size, distribution and seasonality of food sources.

8) Three methods of quantification are listed: longitudinal sampling, latitudinal sampling, and sampling the "Predominant group activity." In this study, chief use was made of a longitudinal sampling technique, since almost all animals studied could be easily identified and followed from a short distance.

9) The approach taken in the presentation of results is described. Part I includes a general introduction and description of the study areas and methodology. In Part II, observations on the ecology and social structure of the study groups in each area are described and considered together in eight sections. In Part III, an attempt is made to integrate the results given in Part II.

Fig. 1. The approximate distribution of the four sub-species, P.v.coquereli, P.v.deckeni, P.v.coronatus and P.v.verreauxi


P.v. deckeni
P.v. coquereli
P.v. verreauxi
P.v. coronatus
N
0
200
miles

PART IB: DESCRIPTION OF STUDY AREAS AND METHODS OF STUDY

INTRODUCTION

Propithecus verreauxi is found in forested areas in the south, west, and north-west of Madagascar. The approximate distribution of the four subspecies, P. v. coquereli, P. v. deckeni, P. v. coronatus, and P. v. verreauxi, is shown in Figure 1.

The first six weeks of the field study were spent surveying in the north-west and south of the island, looking for two ecologically contrasting forests that would be suitable for a long-term study. A further six weeks were then spent habituating selected groups of P. v. coquereli in the north (see Plate I), and P. v. verreauxi in the south (see Plate II), and drawing up a record sheet for their activities.

In this section reasons for the choice of the two study areas are discussed, and the study areas are described. The study groups and the process of habituating them are then described, and finally an account of recording techniques if given.

RESULTS

Selection of study areas

There were three principle considerations involved in the selection of study areas.

a) Abundance of P. verreauxi. For the investigation of inter-group relationships, it was important that the study groups should belong to a coherent population rather than live as totally isolated units. Further, the presence of isolated groups was likely to be a result of persistent hunting. This would probably make the remaining groups very wary and difficult to habituate. The incidence of hunting varied enormously from

region to region, depending on the mores of the tribe living in the area.

b) Condition of forest. Most of the more accessible forests of Madagascar have been disturbed and transformed by man, through wide-scale timbering, slash-and-burn cultivation, cutting for firewood and grazing cattle. Optimally, the study areas would not be subject to such interference, so that animals could be observed living in habitats whose characteristics and stability were not undermined by man.

c) Accessibility of study areas. For a valid comparison of the behaviour and ecology of animals living in two contrasting habitats, observations had to be made in both areas in the wet and dry season. Thus, round-the-year accessibility by car was vital. Carrying in sufficient supplies by foot for a prolonged study would have consumed too much time and money.

Partly because of this prerequisite of accessibility, and partly because of the limited time allotted for surveying, both the study areas finally chosen were, or had been, subject to some direct interference by man. However, P. verreauxi was abundant in both, there was hunting in neither, and the degree of interference appeared to be quite limited (see below).

Northern study area

The northern study area (16° 35' South and 46° 82' East) was situated in the forestry reserve at Ampijoroa. This reserve is in a region known as the Ankarafantsika. The study area itself was about 100kms. from the west coast of the island, and 2kms. from Lac Ampijoroa.

No timbering was permitted in the reserve, and livestock were never seen in the study area. Although not as rich ecologically as some other parts of the Ankarafantsika, this particular area was ultimately chosen for its reliability of access.

Soil in the hill-top study area was extremely sandy, and the small stature of trees was probably a reflection of the poverty of the soil as well as of the age of the forest: apart from the forest's low profile, the usual characteristics of a very young secondary succession (Richards, 1966) were absent. This suggests that the forest had not been disturbed recently. Most trees were between 3 and 13m. in height, with emergents rarely exceeding 21m. Both deciduous and evergreen trees were present (see Plate 3), the former losing their leaves at the onset of the dry season, so that the forest took on the general appearance of an English forest in early autumn (see Plate 4).

Seasonal changes in climate were clearly defined. Petter (1962a) reported the wet season beginning in November, but in 1970-1971 heavy rain began to fall, particularly at night, in the middle of October. These rains continued until the end of March, but little or no rain fell between March and October. Henceforth, months between October and March are referred to as wet season months, and the rest of the year as the dry season. Mean annual rainfall in this area is 1600mm. Maximum and minimum temperatures, recorded in the study area, were 39°C. and 14°C. (For a more detailed analysis of climate, see Pp. 213-16, and Figures 29 and 31.)

The forest contained six prosimian species in addition to P. v. coquereli: Lemur fulvus, Lemur mongoz, Microcebus murinus, Cheirogaleus medius, Lepilemur mustelinus and Avahi laniger.

Southern study area

The southern study area, 24° 85' South, and 46° 50' East, was situated in arid forest 1km. south of Hazafotsy. This was about 1,500kms. from the northern study area. Hazafotsy, a tiny village about 100kms. north-west of Fort Dauphin and 60kms. from the south coast, lay on the north-west boundary of Reserve Nationale No. 11. The River Mananary, a tributary of

the Mandrary, ran for some distance along this boundary after flowing down from the Anosy mountain chain. A spur of low hills adjoining this chain, which rose about 30kms. east of the study area, extended to the west of the chain, so that the study area was enclosed by hills only 4 kms. to the north, south and east. To the west the land was flat.

In the past, the vegetation in this region has been referred to as "bush" (Cabanis et al., 1970). Here it is referred to as "forest," partly to distinguish it from the scrub-bush found over wide areas of southern Madagascar, and partly because "bush" seems an inappropriate term to describe vegetation containing trees up to 21m. in height.

The forest in the study area had not been burnt or felled in recent times, but cattle and goats grazed in it throughout the year. The sparseness of vegetation at ground level may have been an effect of this grazing. Dead wood was cut up by the villagers for firewood: ostensibly, only natural tree-falls were used for this purpose, but in practice some surreptitious felling did go on, the wood then being left to dry out before being cut up. Despite this, however, the forest did not differ much in appearance from that at Evasy, a village 500kms. to the west. (The forest at Evasy was sacred and thus untouched by the local people. Impractical as a study area because of the taboos surrounding it, it nevertheless provided a useful yardstick by which to estimate the effects of human interference on other Didierea forests.)

The forest was dominated by xerophytic vegetation, and particularly by species of the Euphorbiaceae and Didiereaceae families (see Plate 5). Over 80% of the plant species in this forest were endemic, although the overall number of species was lower here than in the north (see Section II). Many species exhibited water-conserving adaptations, such as extreme reduction of leaf-size or huge-girthed "bottle" trunks. Most trees were less than 13m. high and it appeared that, in this area anyway, there was a

critical size beyond which two of the most abundant Alluaudia species present, A. procera and A. ascendens, became top-heavy, with the entire branching super-structure ultimately being torn off the trunk by its own weight. As in the north, many trees in this forest were deciduous and shed their leaves at the beginning of the dry season. Scattered about the study area were clearings where the thin soil did not cover the underlying granite rock; these exposed rock surfaces supported little or no vegetation.

Seasonality was much more marked in the south, and the changeover from one season to the other more abrupt, than in the north. Almost all rain fell in January, February and March. These months are henceforth referred to as the wet season. During the rest of the year, the dry season, there was virtual drought. Periodically, the rains fail altogether, as in 1972. During field work in the south in 1971, very little rain fell outside two ten-day periods when cyclones swept through the region. The low-lying study area was traversed by stream beds that were dry for all but one month, from mid-February to mid-March. Mean rainfall per annum in this area is 600mm. Maximum and minimum temperatures, recorded in the study area, were 44°C. and 8°C. (see Pp. 213-16 and Figures 30 and 31 for a more detailed analysis of climate).

Only two prosimian species other than P. v. verreauxi were seen in the southern forest: Microcebus murinus and Lepilemur mustelinus. Lemur catta vocalizations were heard on one day, apparently from animals moving rapidly through the forest.

Preparation of study areas

In the northern study area narrow trails were cut through the forest running north-south and east-west, at measured 50m. intervals. A minimum of vegetation was cleared in making these trails, and frequently only the paint-marks at 5m. intervals along them betrayed their presence; the marking

system also permitted immediate individual recognition of trails. A precise estimate of the error resulting from inaccurate mapping of trails was not made (c.f. Clutton-Brock, in press). However, all trails were paced and two, where the margin of error exceeded ±10m., were re-cut. (It was assumed that 1 pace equalled approximately 1m.) The shortness of trails (maximum length 450m.) tended to restrict the effect of any errors that may have been introduced by inaccurate compass reading.

The grid system covered the home-ranges of the two study groups, and was expanded where necessary when animals ranged into new areas.

In the south a similar system was used, although with the almost clear forest floor, trails had only to be painted in and little initial clearance was required.

The trails facilitated rapid and quiet movement around the forest in the north, where progress was sometimes hampered by the undergrowth. This was useful during habituation, but of little value subsequently. Habituated animals generally moved quite slowly and could be followed through the middle of squares without difficulty: trails were used only incidentally, when they offered the best vantage point.

In both study areas, the main purpose of the grid system was to plot the movements and ranging patterns of each group and to determine the amount of time the group spent in different parts of its home-range. To this end, optimal square size in the grid system would be the maximum compatible with fairly accurate measurement of total home-range size. This can be determined empirically (Struhsaker, pers. comm.); however, the rationale for the 50m.-sided square used in this study was that it represented the minimum (and thus the most accurate) unit of measurement that could practically be implicated. In effect, the grid divided up each group's home-range into about 36 squares (see Pp.123-32). In future studies, the accuracy of mapping will be increased by plotting the location of the group <u>within</u> each

square rather than simply noting the square occupied. (The drawbacks of the grid system used in this study are further discussed on P.124.)

Habituation of groups

A group was said to be habituated when all its members would approach to within 2m. of me to feed. "Group" habituation is thus to be distinguished from the habituation of single animals within a group. Quantitative records (see Pp. 37,38) were kept only of animals belonging to habituated groups.

Method. When observations were first taken up in the northern study area, stalking was a practical impossibility: cover was minimal, and the forest floor was ankle deep in dead, dry leaves. Thus animals were necessarily followed quite openly, although with a minimum amount of sudden noise or movement; indeed, I tried to ensure that I could always be seen by them. The underlying rationale for this method was similar to that of Stoltz and Saayman (1970) when they were habituating Papio ursinus. Assuming that the flight response of the potential study groups had not been heavily re-enforced through hunting by man, it was felt that if contact could be maintained with the animals for sufficiently long periods of time, their continued inability to "escape," and hence the lack of reward to their flight response, would ultimately result in the extinction of that flight response. Irrespective of the validity of the underlying theory, in practice this method succeeded rapidly.

Groups' initial flight response. Groups were easily located in the early morning when they were sitting high in the trees "sunning" (see Plate 6 and P. 217). After head-jerking (a gesture made in alarm situations - see Jolly, 1966) and low-intensity alarm growling at me intermittently for about twenty minutes, the whole group would briefly give the high-intensity alarm vocalization, the hiccoughing "sifaka," and then split up and flee.

Flight took the form of rapid bounds, either through the top of the continuous canopy, or only 1-2m. above the ground from vertical trunk to vertical trunk. Although the whole group generally fled in approximately the same direction, its members scattered widely as they did so and frequently I lost them completely. However, animals rarely fled far but tended to move 50m. and then hide in dense foliage or, in the south, concealed in the middle of an Alluaudia tree. Once "hidden," animals did not attempt to move until I left: on one occasion, an animal was kept under observation in the fork of a tree from 0700h. until 1630h., at which point observations were abandoned. When I returned to the tree half an hour later the animal had disappeared.

Process of habituation. The most striking aspect of the habituation process was the animals' gradually acquired, apparently almost total indifference to my presence. On the fourth day of observations of each of Groups I, II and III, animals initially reacted to my presence as on previous days, but they moved off more slowly and did not scatter as they did so; for the first time, animals further from me paused briefly to feed. On the fifth day animals did not retreat as long as I remained at least 12m. from them. After two and a half weeks of continuous day-time observation, all animals in all three groups would approach and feed within 2m. of me. Although occasional glances at me demonstrated the animals' general awareness of my presence throughout the study, they seemed to be unaffected by it. Group IV took three and a half weeks to reach the criterion of habituation. The reason for this is not known. There was no difference apparent in the speed with which the different age/sex classes habituated in each group.

In all four groups, habituation took place with reference to individuals rather than to the presence of people generally: they showed an immediate flight response when approached by strangers. My presence one morning in

brightly coloured clothes was responded to by head-jerking, "sifaka" vocalizations and a close "examination" before animals continued with their normal activities, ignoring me as usual.

Study groups

Reasons for restricting number of groups studied. Two neighbouring groups were chosen for study in each area. This sample size provided a compromise between the requirements of one of the aims of the study, and the necessity of sampling enough animals to minimize the possibility of "aberrant" results. The aim was to investigate the effects of differing habitats on the behaviour of P. verreauxi (see P. 2). It was assumed that some variations in behaviour might be of a subtle nature, resulting from very slight differences in ecology. If data had been in the form of surveys of several groups they would have precluded the detailed analysis required to detect such differences. Two groups rather than one were selected in each area, however, because it is acknowledged that extreme limitation of sample size limits the significance of results, and there was enough time to study both in the depth desired.

Criteria for sexing and aging animals. Sex could be determined from the appearance of the genitalia and, in adults, from the presence or absence of the throat gland, found only in males. Although sub-adult and juvenile males performed the rubbing action associated with throat marking (see P. 281) the gland did not appear as a dark strip on their throats as it did in adults.

Since the birth period was very short each year, and synchronized between females in each region (P. 297), gradations in size and, presumably, age of immature animals in each study area were very clear. Further, one infant was traced from birth to the age of seven months (P. 66). Combining knowledg

of the size of an animal at seven months with the knowledge that births occurred at approximately yearly intervals, the ages of immature animals could be inferred on the assumption that each size gradation contained the offspring of a different birth period. It is unlikely that any stage was missed because of the small sample size since P. verreauxi takes only three years to reach maturity.[1] It is assumed that the categories infant, juvenile and sub-adult marked this three-year maturation process.

Animals that were carried part of the time by adult females were sidered as infants. (At seven months, an infant was still occasionally carried by its mother (see Plate 7). No record of development between seven months and one year was obtained. From one year, animals moved completely independently of their mothers.) Animals up to two years old that were completely independent of their mothers were called juveniles. Animals between two and three years old were called sub-adults. It is possible that growth may continue for more than three years before full adult size is reached, and that the sub-adult grade included animals over three years old. However, there were no clear distinctions beyond those described here.

Description of study groups. The age/sex composition of the four study groups at the outset of the study is given in Table 2. Apart from sex and size/age differences, individuals were recognized by variation in features such as coat colour and condition, facial scars, ear notches, broken digits and, in the south, the formation of the dark "cap line" on the head. The absence of this cap in the northern subspecies made recognition much more difficult: in Group I, five adult females could not be consistently identified, though identification on a day-to-day basis was possible through

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[1] Jolly (1966) states that "the 21-month animals are indistinguishable from adults." However the short, highly synchronized breeding and birth season each year and the three easily distinguishable grades of immature animals suggest that maturation must take about three years.

temporary discolorations of fur and bare patches on the tail.

All other animals were recognized individually, and a few examples are given below to illustrate the nature of their individuality. In Group I, adult male GOP had very torn ears, a scarred face and mottled coat, and he spent most of his time on the ground, moving by bipedal hops and lagging as much as 150m. behind the rest of the group. In contrast, adult male N had only one small nick out of one of his ears. In Group II, adult male H appeared almost as battered as adult male GOP, but he moved with other group members and spent no more time on the ground than they did. Sub-adult male YN had a distinctive, dark grey back. In Group III, adult male F, adult female FD and J had very pale brown caps compared with the deep brown of the other three animals in the group. Adult male F's ears were both torn, while adult male P had only one small hole punctured through his left ear. In Group IV, adult male R's right ear was torn while sub-adult male Q's (like those of the sub-adults in other groups) were intact. Both adult females had particularly dark caps, but while adult female FNI's cap line was straight, adult female FI's showed a pronounced "widow's peak."

Observational techniques

Data recording. The northern study groups, I and II, were observed during the dry season months of July and August, 1970 and July, 1971, and during the wet season months of October, November and December, 1970. The southern groups, III and IV, were studied during the dry season months of April, May and June, 1971 and during the wet season months of January, February and March, 1971. Observations on Group III were also made in September, 1970.

One animal was followed for twelve hours each day, from 0600h. - 1800h. This permitted accurate estimation of the amount of time an individual spent in different activities in the course of a day. Each day the age/sex class of the subject was changed so that observations were equally distributed

between the different categories, as well as between different times of day.

Data on most aspects of behaviour were recorded at minute intervals. This was the minimum time interval compatible with recording information in the detail required, and was used in order to follow as closely as possible changes in the subject's activities. Timing was done with a small instrument that emitted a "bleep": observations were recorded on the subject at the moment the "bleep" sounded and, if the subject was not visible, no record was made for that minute. 72 hours of data collected in this way were recorded for each group in each of the months referred to above. Henceforth, the NUMBER OF RECORDS MADE AT MINUTE INTERVALS which an animal spent in an activity will be referred to as TIME SPENT in that activity. These terms are not synonymous, but the latter is used for its brevity.

A 72-hour sample was made in June 1970 and September 1971, recording the activities of all group members visible at half hourly intervals (see P. , "Latitudinal sampling"). This was done in order to investigate the degree of synchronization that existed between the activities of different animals in each group.

A continuous record of social interactions between the subject and any other member of the group was kept. This was feasible because overt social interactions occurred relatively rarely, and permitted the collection of much more data on this aspect of P. verreauxi behaviour than would have been assembled using the time-sampling technique. Descriptive notes of other rarely occurring events, such as responses to aerial raptors, were also made throughout the study.

Types of information recorded. There are obvious dangers inherent in the premature categorization of behaviour patterns, and six weeks were spent observing the study groups before a data sheet was drawn up. However, the nature of the data recorded was such that it did not involve a major

interpretative role being played by me. The greatest source of error was probably the estimation of spatial measures such as "height of subject above ground" (but see P. 84).

Data on the subject animal were collected under 15 headings, or categories. Many of these categories contained several subdivisions. Each subdivision was numbered, so that data sheets apparently contained numerical information; in fact, many of these numbers were merely a shorthand for descriptive categories. These categories, and their subdivisions, are listed and described below in five groups. Further description and operational definitions of behavioural categories are given in context in the appropriate section.

a) <u>Identity and location of subject</u>

1) Identity of subject animal. All animals were individually recognized and allocated an identifying number on the data sheet. This category remained constant throughout the day unless contact was lost with the subject.

2) Time of day at which recording was made. Unless some disturbance interrupted recordings, this record ran from 0600h. - 1800h. at minute intervals.

3) Square of the grid occupied by the subject. Squares were identified by the markings on the trails surrounding them.

4) The subject's height above ground. The following subdivisions were used:

on the ground
off the ground - 1½m.
1½m. - 3m.
3m. - 5m.
5m. - 7m.
7m. - 10m.
10m. - 13m.
over 13m.

This measure was subject to some inaccuracy in that subdivisions were discriminated between by eye alone, but the inaccuracy was within the

general margin of error of the study.

5) Whether the subject was in the sun or the shade.

b) Subject's activity and related factors

1) Subject's activity. Activities were recorded in the following, mutually exclusive subdivisions:

resting
feeding
foraging
moving
leaping
interacting
self-grooming
allo-grooming
scent-marking

Operational definitions of these activities are discussed in the appropriate contexts.

2) Subject's posture. P. verreauxi has a very wide range of postures associated with the whole spectrum of locomotor patterns of which the species is capable. These postures constitute a continuum which is difficult to divide up meaningfully into discrete categories. However, a rudimentary classification was required by which to estimate regional and inter-individual differences, and eight basic postural categories were finally formulated. It should be stressed that these categories all included some variation. The classification given below should not be considered as a full analysis of the range of postures seen; the species' locomotor totipotentiality (Prost, 1965) was wider than suggested by such a restrictive classification:

a - characteristic vertical clinging and leaping posture on a vertical support (Plate 2).

b - sitting on a horizontal support (Plate 8).

c - hanging by arms (Plate 9).

d - hanging by legs (Plate 10).

e - hanging by one arm and one leg.

f - lying along a horizontal support (Plate 11).

g - clinging by arms and legs under a network of twigs, with minimal curvature of the vertebral column.

h - hanging under a branch in a sloth-like position, with the vertebral column curved, weight supported by legs and one arm (Plate 12).

3) Subject's substrate. Five different types of substrate were categorized. These related closely to the structural components of trees in both study areas:

a - ground.

b - main (greater than 6cm. in diameter) trunk or vertical branch.

c - main (greater than 6cm. in diameter) horizontal trunk or branch.

d)- branches less than 6cm. in diameter.

e - twigs less than 1½cm. in diameter.

The division of substrates in this way was done by eye, so there may have been some inaccuracy, but it was within the limits of accuracy of the study.

4) Food species, if the subject was feeding. All food species were numbered, and the number recorded in this category if the animal was feeding. The part of the food species being eaten was described separately.

5) The distance travelled, if any, by the subject in the preceding minute. This again was subject to inaccuracies resulting from measurement by eye alone.

c) Group dispersion

1) Proximity of the subject's nearest neighbour. Five categories of proximity were established:

physical contact
1 - 2m. to nearest animal
2 - 3m. to nearest animal
3 - 6m. to nearest animal
over 6m. to nearest animal

2) The identity of the subject's nearest neighbour.

d) Communication

1) Vocalizations, if any. P. verreauxi's vocal repertoire is characterized

by a series of easily recognizable calls, between some of which there were intermediate vocalizations. Thus seven subdivisions, representing seven types of vocalizations, were formulated. On occasion, the allocation of "intermediate" calls to these subdivisions was fairly arbitrary, but they constituted a small proportion of total calls made. Nomenclature follows Jolly (1966):

low growl
sifaka
roar
purr
coo
locomotor grunt
spat

These calls are referred to where relevant throughout this thesis, but a more detailed analysis of their structure and function is still in preparation.

2) Whether the subject had scent-marked (see Section VIII) in the preceding minute. This category did not record the frequency of scent-marking within each minute.

e) Environment

1) The weather was described in five general subdivisions while data were being collected on the animals. These subdivisions were:

rainy
overcast with no wind
overcast with wind
sunny with no wind
sunny and windy

In addition, the temperature at 0600h. and 1800h., and the maximum/minimum temperatures for each twenty-four hours, were recorded from a thermometer hung in the shade in the middle of each study area. Rainfall data were supplied by meteorological stations, located within 30kms. of each study area.

Equipment used. Tape recordings were made with a portable Tandberg 11P tape recorder and a Sennheiser directional microphone. Photographs were

taken with a Praktica Nova 1B and a 35mm. lens or 135mm. telephoto lens. Observations of the animals were made generally with the naked eye or, when they were moving higher in the trees, with Leitz Trinovid 8x42B binoculars.

Analysis of vegetation

A vegetational analysis, sampling the forest throughout each study area, was carried out in the course of the field study. The techniques used in this analysis are described in Section II.

SUMMARY

1) P. verreauxi is widely distributed in Madagascar, and six weeks were spent surveying for a suitable study area.

2) The three principle considerations involved in the selection of study areas were abundance of P. verreauxi, condition of the forest, and accessibility of the forest. The two study areas finally selected fulfilled the first and third criteria, but were, or had been, subject to some interference by man. However, most of the easily accessible forests in Madagascar have been transformed by man, and the degree of interference appeared to be quite limited in those selected as study areas.

3) The northern study area was at Ampijoroa, in the Ankarafantsika. The forest contained both deciduous and evergreen trees. The relative poverty of the sandy soil may have contributed to the generally low profile of the forest. Most rain fell between October and March. Six prosimian species in addition to P. verreauxi were seen in the study area.

4) The southern study area was at Hazafotsy, in the extreme south-east of the island. The forest was dominated by xerophytic vegetation, and over 80% of the plant species were endemic. Exposed rock surfaces supporting little or no vegetation were scattered about the study area. Season-

ality was extremely marked, with almost all rain falling in January, February and March. Only two prosimian species other than P. verreauxi were seen in this forest.

5) Trails were cut through both study areas running north-south and east-west at measured 50m. intervals. A marking system permitted immediate individual recognition of trails. The main purpose of this grid system was to plot the movements and ranging patterns of each group and to determine the amount of time the group spent in different parts of its home-range.

6) A group was said to be habituated when all its members would approach to within 2m. of me to feed. Quantitative records were kept only of animals belonging to habituated groups. Animals initially responded to my presence by giving an alarm call, splitting up and fleeing. I attempted to maintain contact with the animals as they fled, so that their flight response would not be rewarded. When contact was established on the fourth day, with each group, animals fled more slowly, and within 3½ weeks all four groups were habituated.

7) The number of groups studied was restricted to two in each area so that the relationship between single groups and their environment might be studied in detail. Two groups rather than one were studied in each area because the extreme limitation of sample size inevitably reduces the meaningfulness of results, and there was enough time to study both in the depth desired.

8) Sex could be determined from the genitalia and presence or absence of a throat gland. Clear-cut gradations in the size of immature animals were a result of the highly synchronized and seasonal breeding season, and permitted an easy classification of animals into infant, juvenile, sub-adult and adult categories.

9) Individuals could be recognized by variation in features such as coat

colour and condition, facial scars, ear notches, broken digits and, in the south, the formation of the dark "cap line" on the head.

10) One animal was followed for 12 hours each day, and recordings were made on it at minute intervals throughout this period. Each day, the age/sex class of the subject was changed so that observations were evenly distributed both between age/sex classes and different times of day. 72 hours of data collected in this way were recorded for each group in each study area over a period of six months. Observations were made in both study areas equally in the wet and dry seasons.

11) A 72-hour latitudinal sample, recording the activities of all group members visible at half hourly intervals was made.

12) Social interactions were relatively rare and a continuous record of any interaction between the subject and another group member was kept.

13) Quantitative data were collected on five main factors: the identity and location of the subject, the subject's activity and related factors, group dispersion, communication, and the environment.

14) A vegetational analysis was also carried out. Techniques employed in this analysis are described in Section II.

Plate 1. Propithecus verreauxi coquereli: adult female.

Plate 2. Propithecus verreauxi verreauxi: adult female with seven month old infant.

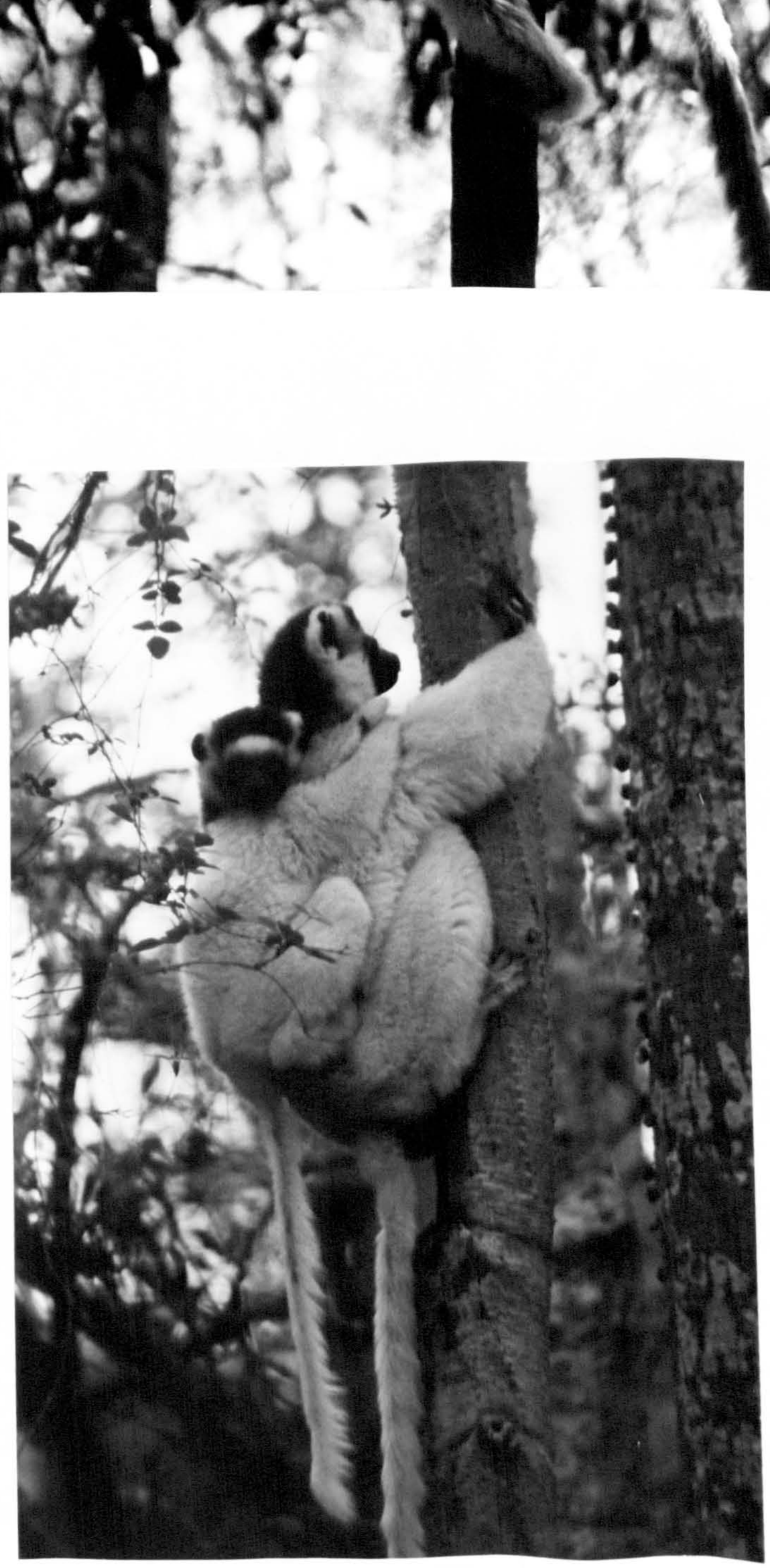


Plate 4. Northern Study Area (Ampijoroa), July 1971

Plate 3. Northern Study Area (Ampijoroa), October 1970

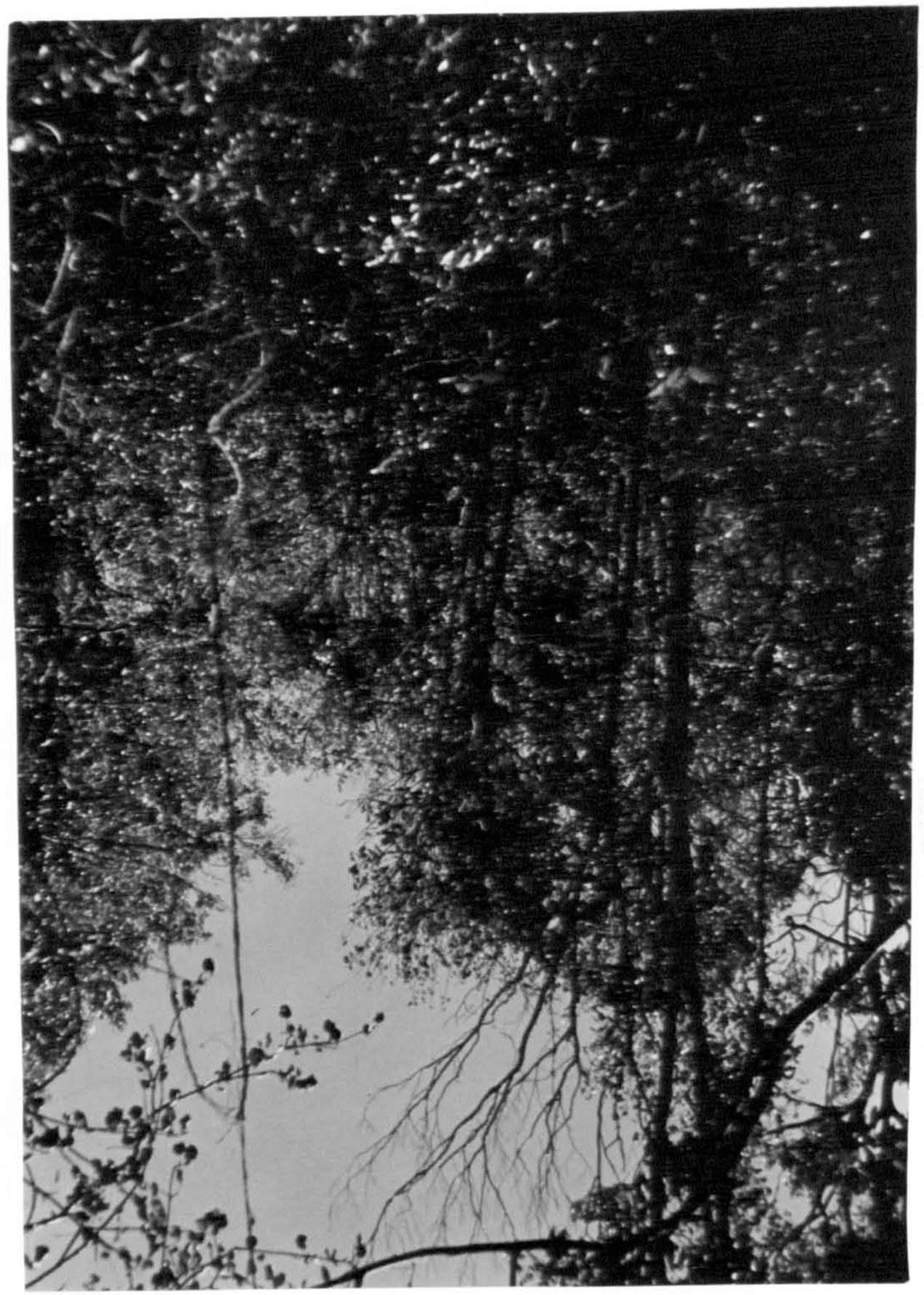


Plate 5. Southern Study Area (Hazafotsy), September 1970.

Plate 6. Group III exhibiting "sunning" behaviour.

Plate 7. Adult female crossing clearing bipedally, with seven month old infant on her back.

Plate 8. Sub-adult male feeding in posture (b) - sitting on a horizontal support.

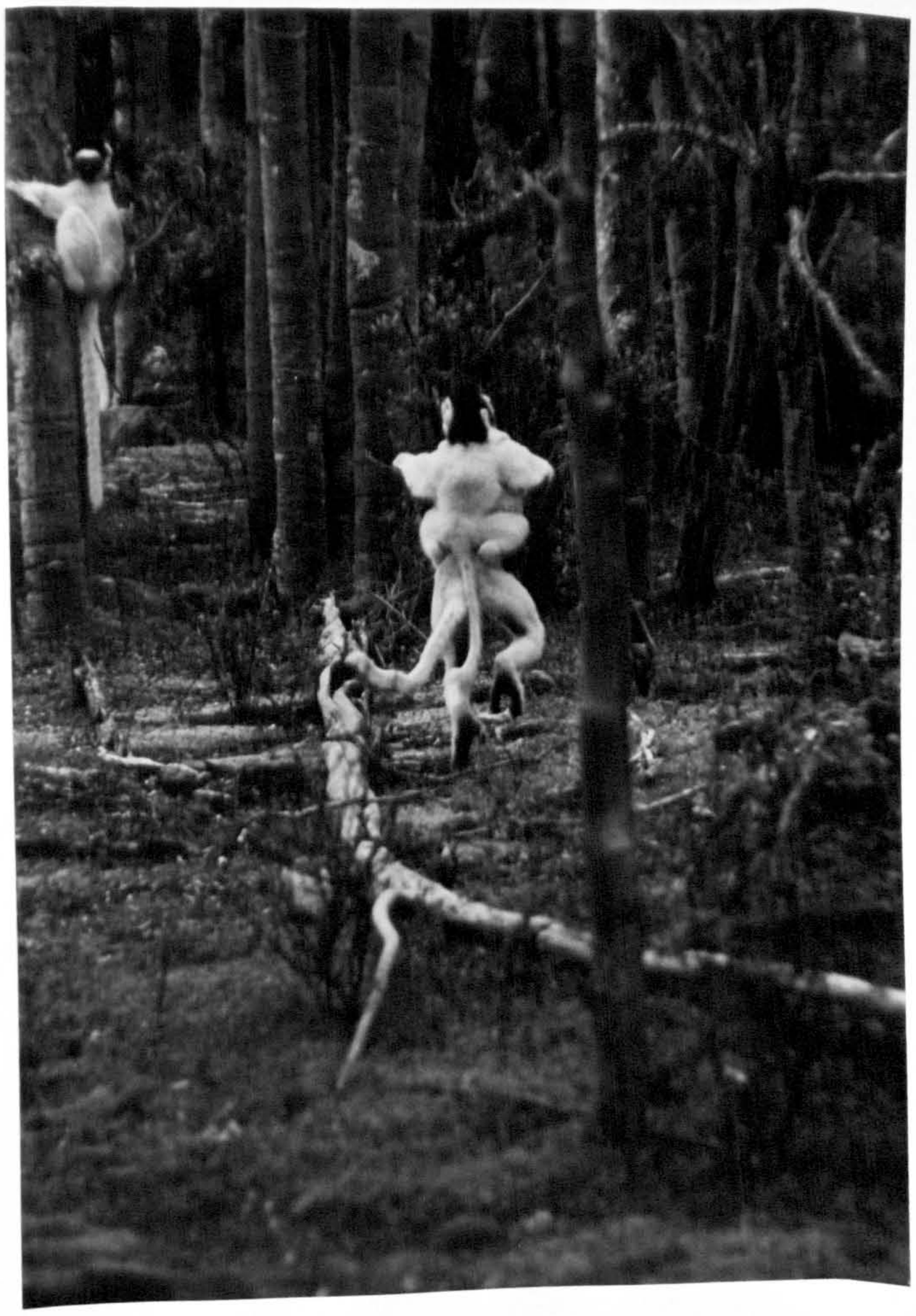


Plate 9. Sub-adult male in posture (c) - hanging by arms.

Plate 10. Sub-adult male in posture (d) - hanging by legs.

PART II:

OBSERVATIONS ON THE ECOLOGY AND SOCIAL ORGANIZATION OF PROPITHECUS VERREAUXI

SECTION I: GROUP COMPOSITION AND POPULATION DYNAMICS

INTRODUCTION

Areas sampled

One thorough census of a small population of P. verreauxi was made. This census, carried out at Berenty with the assistance of T. T. Struhsaker in September 1971, covered ten groups living in gallery forest. These groups were chosen for the census in preference to groups in either of the study areas set up for the present project, because not only did they provide information on group size and composition, but also on changes in these factors through time: this was the fourth census to be made on this population in eight years (see Jolly, 1966, 1972). Two, much more limited surveys were conducted at Evasy and Ejeda.

In the study areas, most time was taken up with a detailed investigation of four groups, and generally the composition of other groups was established only if and when they encountered the study groups. Information on the processes by which group composition changed, that is on births, male mobility and deaths, came almost exclusively from the four study groups.

Limitations of data

Only reliable counts are presented. These came from groups containing at least one marker animal, so that group size could be checked repeatedly. A count was considered to be reliable if on three separate occasions the same number of animals were counted in a group. This method assumed that apparent changes in group size were due to observer error rather than to real changes within the group; although this assumption may not have been justified in every case, it did minimize the effect of under-estimates and was adhered to for this reason.

TABLE 1: Counts and partial analysis of the age and sex composition of all groups observed in each study area, and at Berenty, Evasy and Ejeda.

Locality & Date	Adult Male	Adult Female	Sub-Adult	Juv.	Inf.	Total
Ampijoroa (northern study area) July'70	*?	5				7
	*1	1	1(♂)	1(♂)	1	5
	?	1				4
	?	2	1		1	7
	1	2		1	1	5
	?	3				5
	?	5	1		1	10
	15	19	3	2	4	43
						6
		Adult				5
		Composition			1	4
		Unknown				4
					1	4
Total number in 12 groups						66
Hazafotsy (southern study area) Sept.'70	*?	2	1(♂)	1(♂)	2	8
	*1	2	1(♂)		2	6
	?	1			1	4
	1	2		1	1	5
	?	4	1		1	8
	8	11	3	2	7	31
						8
		Adult				6
		Composition				5
		Unknown				5
						3
Total number in 10 groups						58

* study groups

TABLE 1 Cont.

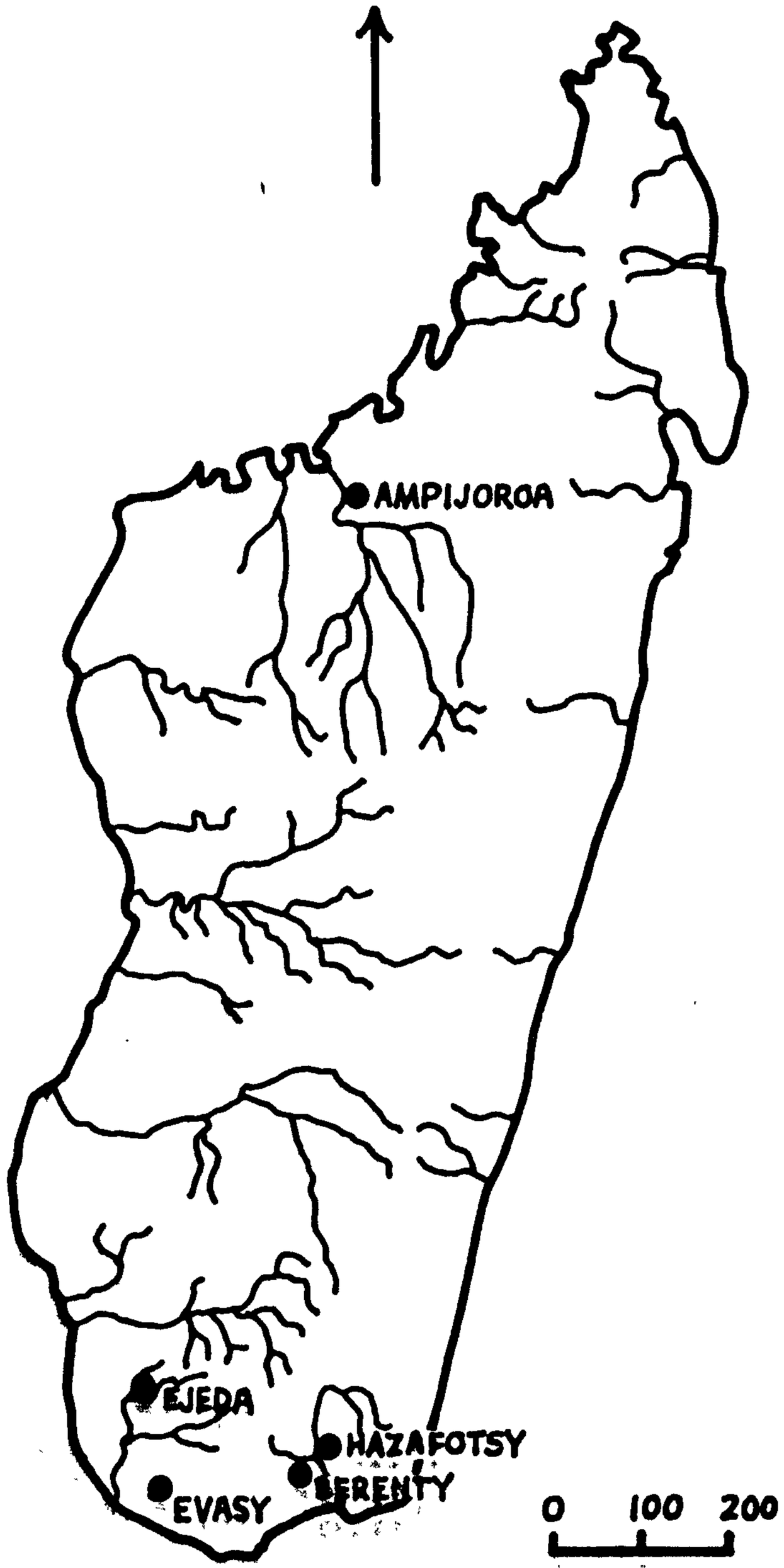
Locality & Date	Adult ♂	Adult ♀	Sub-Adult	Juv.	Inf.	?	Total
Berenty Sept.'71	?	?		1	2		8
	?	1		1	1	1	7
	2	1					3
	?	?			S-a:1		7
	1	5			1	A:1	8
	?	?					5
	2	?		1	2		7
	?	4		1	2		9
	?	?		1	2		9
	2	1		1		A:1	5
	(*?)						(2)
Totals for 10 groups	24	24		6	10	4	68

*These two males moved together in the area occupied by the ten groups listed.

Evasy May'70		10
	Adult	7
	Composition	7
	Unknown	6
		5
		4
		4
		4
Total number in 8 groups		47

Ejeda May'70		7
	Adult	7
	Composition	
	Unknown	
Total number in 2 groups		14

Fig. 2. Locations at which surveys of P.verreauxi were made.


AMPIJOROA
EJEDA
HAZAFOTSY
EVASY
BERENTY
0 100 200
MILES

Much of the surveying was done during the first two months of the study, when my lack of experience made identification of age/sex classes more open to error than it later became. Most of these early estimates of group composition have been omitted, therefore, and only reliable total group counts from this time are included.

RESULTS

Group counts

At Ejeda, in the south-west of the island, the habitat surveyed was gallery forest along the banks of the River Linta. The forest at Evasy, situated in the extreme south of the island, was much like that in the southern study area at Hazafotsy, dominated by Didierea and Euphorbia species (see P.30). The gallery forest at Berenty, lining the River Mandrary, has been described by Jolly (1966). The locations of these forests are shown in Figure 2.

The results of surveys made are given in Table 1. Group size ranged from 3 - 10, excluding the two adult males found together at Berenty. Statistical analysis showed no significant difference in group size between Ampijoroa, Hazafotsy, Evasy and Berenty. Significant differences might become apparent, however, if comparisons were made between much larger samples from each area, and the small sample size used here makes the results inconclusive. Mean group size varied as follows:

5.0 (Ampijoroa - northern study area - n=12)

5.1 (Hazafotsy - southern study area - n=10)

5.8 (Berenty - n=10)

5.9 (Evasy - n=8)

7.0 (Ejeda - n=2)

No infants were present in groups at Ejeda and Evasy, because both these

TABLE 2: Initial composition of the four study groups and subsequent changes.

Group	July 1970	Oct. 1970	Dec. 1970	July 1971
I	5 AQ♀	5 AQ♀	4 AQ♀	4 AQ♀
	AO♂ GOP	AO♂ STR	AO♂ BE	AO♂ BE
	AO♂ N			2 Infs.
II	AQ♀	AQ♀	No change	AQ♀
	AO♂	AO♂		AO♂
	SA O♂	SAO♂		SA O♂
	J	J		J
	Inf.			Inf.
	Sept. 1970	March 1971*	June 1971	Sept.1971
III	? AQQ♀	? AQQ♀		?AQQ♀
	? AOO♂	? AOO♂	No change	2AOO♂
	SA O♂	SA O♂		SA O♂
	J	J		J
	? Infs.			2 Infs.
IV	?AQQ♀	? AQQ♀		2AQQ♀
	AO♂ R	AO♂ INT	No change	AO♂ INT
	SA O♂	SA O♂		SA O♂
	? Infs.			Inf.

*AO♂ P's brief detachment from Group III and association with Group IV is not recorded here.
Where group members are not individually named, it can be assumed that their identity remained the same.

areas were surveyed just prior to the highly seasonal birth period. Comparisons of group size and the calculation of mean group size have therefore been made excluding infants, in order to compensate for seasonal differences in the timing of surveys.

Changes in group composition

The changes in group composition discussed below are summarized in Table 2.

Births.

a) Northern study area. One infant was born in Group II in 1970 (see also P.65), but no infants were born to any of the five adult females in Group I that year. Five other infants, each in a separate group, were known of in the area. These births occurred during June and July (for a further discussion of the timing of the birth season, see P. 297). When observations were taken up in October after a six week interval, the Group II infant and all but one of the other infants had disappeared. The infant mortality rate for 1970/1971 was therefore approximately 84% (n=6).

In 1971, the Group II female produced another infant, and two females in Group I produced infants. It should be noted that there was at least a two day interval between the appearance of these two infants, but after the second birth the two mothers frequently 'baby sat' for each other, for periods of up to five hours. On these occasions, one mother would suckle and carry both infants, leaving the other to move and feed unimpeded. Unless the discrepancy in the times of birth had been known, it might have been thought that these infants were twins, and that one of them was taken over from time to time by a foster mother. No evidence of twinning was found in the course of the study. Since observations ended in the north in July 1971, the survival rate of these 1971 infants is not known.

b) Southern study area. In September 1970, all the adult females in Groups III and IV were found with infants. These infants had probably been born towards the beginning of August: this was inferred from their size and relative independence. When observations were resumed in January 1971, only one infant remained, belonging to adult female FI in Group IV. However, this infant finally disappeared too during a cyclone in mid-February. Infant mortality in the groups sampled in 1970/1971 was thus 100% (n=4).

In August 1971 infants were born to the two adult females in Group III but only to adult female FI in Group IV. Here again, it is not known whether these infants survived.

c) Berenty. In 1971, ten infants were found in the ten groups censused. Four groups had no infants at all, four had two infants each, and the remaining two groups one infant each. Six juveniles that had been born the previous year were counted. Since Jolly (1972) recorded 10 infants in 1970 in what were probably the same ten groups as those censused in the present study (see P.71), a 40% mortality rate among infants in this area can be inferred over the period 1970/1971. This compares with 29% (two infants out of seven surviving at the end of the first year) for 1963/1964 (Jolly, 1966).

d) Birth process. One birth was witnessed during the study. The Group II female had been followed all morning on June 17th 1970 and, after a normal feeding bout, at 1435h. she moved on to a wide horizontal bough about 16m. from the ground. She began repeatedly licking her ano-genital region, leaning forward to do so with her legs stretched out and apart in front of her. At this time, she was approximately 13m. away from other members of the group, who continued to feed and forage. At 1517h. the infant was seen crawling up the ventral surface of its mother, towards her left arm-pit. (It may be significant that the nipples are located in the arm-pits.)

Severance of the umbilical cord was not seen. The mother licked her infant all over for about 10 seconds and then continued to lick her genital region. She was seen tugging part of the afterbirth from her vulva with her teeth, and then holding it in her hand and eating it; at this point, a few drops of liquid fell out of the tree - whether this was blood or amniotic fluid was not established - but this was the only moment at which anything was seen to fall from the tree. Half an hour later, the mother was seen eating another piece of afterbirth, and it is likely that the whole afterbirth was consumed: no traces of it were subsequently found.

At 1530h., the mother moved off, swinging along under a branch, suspended by her arms. She offered no assistance to her infant, who clung transversely across the lower part of her ventral surface, and rapidly moved about 20m. to catch up with the rest of the group, once leaping a 7m. gap between trees to do so. Although the juvenile and adult male came and sat in physical contact with the mother, they otherwise ignored her and her infant; this contrasted strongly with their subsequent behaviour, for the mother and her infant later became the centre of attention for other members of the group.

The mother continued to lick her genital area and her infant alternately until sunset. She was also seen holding the lower part of the infant's body in her left hand, putting the umbilical cord into her mouth with her right hand, and pulling at it with her teeth.

Deaths.

a) Alarm calls. P. verreauxi's vocal repertoire includes a strident alarm call. This was usually initiated by one animal and then taken up almost simultaneously by the whole group, and occasionally by groups in the close vicinity. The call was sometimes accompanied by a fairly stereotyped locomotor response: as the alarm "roaring bark" was given, animals moved rapidly from the periphery of trees on to the central vertical trunk. As

they moved inwards, animals tended to back down towards the ground, looking up at the sky as they did so.

Jolly (1966) postulates that this alarm call is specifically directed at raptors, and that ground predators are mobbed to the accompaniment of the "sifaka" vocalization. This she describes as "...a bubbling groan, with...mouth shut, ended by an abrupt syllable click with mouth open, lips covering teeth (Andrew, 1963b 'chicken-like cluck'; Petter, 1962a 'omb-tsit') ..." This vocalization, the "sifaka," was always directed at me by unhabituated groups, but on the two occasions when my assistant was attacked by unhabituated groups, the roaring bark vocalization was given, and on one occasion when a snake was found eating an adult Microcebus murinus, the animals also gave a roaring bark. Thus, this vocalization is not reserved for aerial predators only.

Correlations between the existence of alarm calls in a species and predation pressure on that species should be made with caution. Cartmill (1972) has commented "...unless these calls (roaring alarm barks) are another Eocene survival, these Malagasy VCLs must be subject to predation..." However, both chimpanzees and gorillas have alarm calls (Clutton-Brock, pers. comm.) although predation pressures are probably minimal (Van Lawick Goodall, 1968; Schaller, 1963). While it could be argued that, without such calls, predation pressures on these species would increase, it seems more plausible that they are an adaptive response drawing attention to sudden unexpected stimuli. There is some evidence that the roaring alarm bark serves this function in P. verreauxi: the northern study groups always gave an alarm call in response to the sound of lorries passing on the main road 3kms. away. Thus, the existence of the alarm call does not in itself denote significant predation pressure on P. verreauxi.

b) Possible non-human predators. The pressures of predation on the lemurs of Madagascar have generally been held to be unimportant, since

there are no large predators on the island. From observations in this study, it is inferred that P. verreauxi may have three non-human predators: aerial raptors, constrictor snakes and the Viverrid, Cryptoprocta ferox.

In both birth seasons witnessed, there was a critical period about one month after their birth when infants grew more and more adventurous, and their mothers less and less attentive, with the result that the two might become separated by as much as 4 - 5m. At this time, the infants were still extremely ungainly and slow-moving and would probably be ill-camouflaged, easy prey for aerial raptors. The vocal and locomotor response to the passage of these birds substantiates this idea (with the reservations mentioned on P.67). There were two species of large raptors in both study areas: Polyboroides typus, and Gymnogenys radiata.

A snake, Ithycyphys miniatus was noticed by Group I in the northern study area while it was strangling an adult Microcebus murinus. After giving the roaring bark alarm, the group sat down about 7m. from the snake and watched silently for 25 minutes while the snake swallowed its catch. The group then moved away and resumed feeding. It is possible that P. verreauxi infants, at about one month, could also be vulnerable to such snakes.

A third potential predator on infants, and possibly even on adults, particularly the old or diseased, is the carnivorous Fosa, Cryptoprocta ferox. Nests of Fosa young have been found in Baobab trees in the south-west, with P. verreauxi bones strewn at their foot (Albignac, pers. comm.). These could have been scavenged, but reliable, eye-witness reports given by two villagers spoke of prolonged fights between adult P. verreauxi and the Fosa.

c) Relations with man. Undoubtedly the most important single predator of adult P. verreauxi is now man. Although protected by law, these animals are hunted for sport and for food in many areas.

Groups made two attacks on my assistant (c.f. Rand, 1935): on both

occasions, he had stalked an unhabituated group to within a few metres. It is plausible that he, as "predator," having approached to within the groups' flight distances, their response was to attack rather than to flee. There was, I think, no doubt that in both instances the groups pursued and attempted to attack, rather than simply to mob, my assistant before ultimately being repelled.

d) Disease. On 18th October 1970, a female aged 3 - 4 years (Albignac, pers. comm.) from Group I was found sitting curled up in a ball on the ground. She offered no resistance to being picked up by me, and died two days later. Subsequent bacteriological analysis did not reveal the cause of death, although numerous non-pathogenic protozoans were found in the red blood cells in the kidney (for a further discussion see Uilenberg et al., in press).

e) Other factors. Many factors in addition to predation and disease probably contribute to infant mortality. Deaths may occur soon after birth due to congenital defects, and during the first few months of life through the drying up of the mother's milk, or through falls resulting from the infant's clumsiness when moving alone through the trees or from a failure to cling firmly enough to the mother's fur when being carried.

It is possible that the Group IV infant that disappeared during the week of the cyclone in mid-February 1971 caught a cold or some form of Pneumonia as a result of the continuously low temperatures and persistent rain during that period.

Large amounts of fur were found in the middle of Group I's home-range in October 1970 when observations were resumed there, and males GOP and N had disappeared from the group. It is likely that the fur belonged to one of these animals. In view of the apparent old age and generally reduced mobility of adult male GOP (P.37), it is probable that these were his remains. It is possible that this seemingly aged animal died from "natural

TABLE 3: Composition of known groups at Berenty, taken from censuses made by Jolly in September 1970 and by Struhsaker and Richard in September 1971.

Year	Group's Name	Adult Male	Adult Female	Juv.	Inf.	Total
'70	UP	2	4		2	8
'71	BLIND	3	3			6
'70	DE	2	2		1	5
'71	KINK	2	2	1	2	7
'70	BN	3	3		2	8
'71	LEN	2	2	1	2	8
'70	PT	3	2		2	7
'71	TWINS	3	3	1	2	9
'70	ST	2	1			3
'71	BLEN	2	1			3
'70	SE	2	1			3
'71	2 AOO	2				2
TOTAL, 1970		14	13	-	7	34
TOTAL, 1971		15	11	3	6	35

causes" rather than from disease or predation.

In the south, adult male R was driven out of Group IV after receiving severe wounds in a prolonged fight during the mating season (see P. 293) It is not known whether male R subsequently lived alone, or joined another group, or indeed died of his wounds. If the fights witnessed were characteristic of some inter-male interactions in the mating season, it is highly likely that males may die as a result of wounds incurred at this time.

Other factors causing change in group composition.

a) Male mobility in mating season. During the mating season in the south, adult male R was ousted from Group IV (see above). His successor was in turn ousted by another intruding male, who remained in Group IV until the study was terminated the following September. These fights and replacements are described in more detail in Section VIII.

b) Male mobility outside mating season. In June 1970, two adult males were present in Group I. By October, both had disappeared from the group and a new male was present, adult male STR. At the beginning of December another male, BE, began moving on the periphery of Group I; as with adult male STR, it was not known whether he had come from another group, or whether he was a solitary, wandering male. Members of Group I made no attempt to chase him away, nor did he try to drive off STR. When observations were subsequently resumed after a week's interval, STR had disappeared from Group I and BE was well integrated into the group. There was no evidence in the form of recent wounds to suggest that he had had to fight his way into the group.

Stability of groups at Berenty. Group size and age/sex composition of P. verreauxi at Berenty in 1971 differed very little from the previous year. Table 3 compares some of the results of Jolly's census in 1970 (see Jolly, 1972) with the census carried out in 1971. Groups from 1970 were re-identified

in 1971, although they were initially given new names, by matching up the geographical location of their home-ranges in the two years, and by identifying certain distinctive "marker" animals, described in detail by Jolly (pers. comm.). Only groups whose 1970/1971 identity was confirmed by these two criteria are included in Table 3. The similarity of the 1970/1971 results agrees with Jolly (1972),wwho returned to Berenty in 1970 after a six-year absence and found "...the number, composition, and spacing of troops, as well as spacing behaviour, seemed unchanged..." Further, she reported that "...four animals (two adult males and two adult females), out of a total of 36 known in 1963/1964 could be recognized in 1970, and were in the same home-ranges, including a mother who had infants in 1963, 1964, and 1970..."

While the evidence from Berenty suggests that there was considerable stability in group size and age/sex composition, it does not in most cases demonstrate whether the actual identity of animals comprising groups remained the same. However, since four adults were re-identified in 1970 in their 1963/1964 home-ranges (Jolly, 1972), and since at least one animal from each of ten groups in 1971 was recognized from Jolly's descriptions in 1970, it is likely that at Berenty fully mature animals tend to remain in the same geographical location and, probably, the same group.

DISCUSSION AND CONCLUSIONS

The implications for P. verreauxi's social system of group size and composition

P. verreauxi live in small units of highly variable composition. While the overall socionomic sex ratio approached 1:1, in a given group there could be a striking excess of males or females. Further research would probably reveal even greater variation in group size and composition: in the west of the island, reliable counts have been made of a group containing 13 animals,

including 5 adult males, 5 adult females and 3 infants, and another group containing 7 adult males, 2 adult females, and possibly a further two peripheral males (Sussman, pers. comm.).

If a system of strict family groups similar to that found in Hylobates lar (Ellefson, 1968) had existed, obvious tension would have been present between adult and sub-adult males. No sign of such tension was found, the frequency of aggression between these age/sex classes being no higher than that between other group members (see Section VII); young males were not driven from the group by the adult male (c.f. H. lar, Ellefson, 1968). Further, there was direct evidence of (probably peaceful) group interchange by males, and of males mating with females belonging to other groups. Thus, the behavioural evidence and the data on group composition confirm that these groups can by no means be considered simply as "families" containing parents and offspring.

The only persistent tension seen between two animals occurred between the two adult males in Group III (see Section VII). These were also the only two adult males in their prime found together in one group, considering only the four study groups. On this basis, P. verreauxi might be allocated to an "age-graded-male troop" system (Eisenberg et al., 1972). However, fully adult males of apparently "roughly equivalent age" moved together in groups without comparable signs of tension being apparent at Berenty (Jolly, pers. comm.). Thus, the explanation in the case of the two Group III males probably lies in the nature of the personal relationship between them rather than in a generalized pattern of behaviour between adult males.

Petter and Peyrieras (in press) state that "...with the Sifakas, as with the Avahi (i.e. in all the Indriidae), the groups would normally have a strictly family basis....but in zones which are more or less degraded or transformed...the family groups are modified to form larger groups...degradation of the environment favours the formation of larger groups..." This view

can be criticized on at least three grounds:

a) 'Large' groups of P. verreauxi were found at Evasy, where the forest was both untouched and extensive, as well as in all other areas surveyed.

b) A self-replicating family group system must incorporate behavioural mechanisms leading to the dispersal of juvenile and sub-adult animals from the maternal group, such as have been reported in the gibbon (Ellefson, 1968). No trace of such mechanisms was found in the relatively flexible social system investigated in the present study.

c) Degradation of the environment need not necessarily favour the formation of large groups. The growing body of literature attempting to relate primate social structure to ecology was surveyed in Part IA. One of the most important points to emerge was that crude ecological categories such as "forest," or "savannah," are inadequate descriptions if social structure is to be meaningfully correlated with ecology. Similarly, here, to speak simply of "degraded forest" as an ecological category is an oversimplification: both the nature of the forest and the degradation that has taken place may vary. The formation of larger groups is likely to be a function of many factors, including predation pressures, and the size, distribution and seasonality of food resources. These factors may vary independently from region to region, in degraded as well as primary forests.

P. verreauxi groups should be considered as foraging parties of mutually familiar animals rather than as reproductive units. While ecological factors may determine the upper limit of group size, selective pressures have apparently not operated to produce a "norm" of group composition such as is found in many other primate species (Carpenter, 1934; Mason, 1968; Kummer and Kurt, 1963).

Socionomic sex ratio

"...In 1970 as in 1963-1964 there were more adult males than adult females,

a peculiarity which remains unexplained..." (Jolly, 1972). At Berenty in 1963, Jolly counted 23 males and 15 females in 10 groups of P. verreauxi: in 1964 she counted 24 males and 17 females, and in 1970 the results were 23 and 22. The 1971 census carried out during this study produced figures of 26 and 24.

Jolly (1966) postulated that the discrepancy in the sex ratio might be a consequence of males living longer than females. This theory was based on the presence of two "old" males who were balding, and had deeply sunken faces in the 1963/1964 study. No females were seen in this condition. In a discussion on breeding lemurs in captivity, Basilewsky (1965) commented "The sex ratio in the group always shows a significant majority of males. This can be established without any doubt, particularly easily in L. macaco with its marked sexual dimorphism, but it is also true for L. catta and most other species." He did not specify whether this referred to the sex ratio at birth, in captivity, or to group composition in the wild, nor did he offer any functional explanation for this observation.

The results of this study confirm Petter's (1962a) findings of an approximately 1:1 sex ratio in P. verreauxi, and suggest that general theories of greater male longevity, differential infant mortality, or an unequal sex ratio at birth, are superfluous. The hypothesis that males lived longer than females had already been undermined by the presence of an "old" female at Berenty in 1970 (Jolly, 1972), and a female of similar appearance was also seen in the northern study area during this study. It should further be noted that baldness and "sunken faces" may be symptomatic of disease or malnutrition rather than old age. Positive evidence from three sources indicates that the excess of males at Berenty in 1963 was a temporary, and atypical, phenomenon. Firstly, since 1963 there has been a persistent trend towards a 1:1 sex ratio at Berenty: the initial 1:0.65 ratio modified to 1:0.71 in 1964, and to 1:0.96 and 1:0.91 in 1970 and 1971. Secondly, the

sex ratio in the northern study area in known groups in the present study was 1:1.2. Finally, in the southern study area the ratio was 1:1.38.

Two interpretations of the 1971 "excess" of males at Berenty are plausible: the population may still have been recovering from the gross, and abnormal, excess present ten years previously. Alternatively, it could be argued that the population had already regained its equilibrium and that the "excess" represented merely one of the minor departures from this equilibrium that would be expected at a given moment in any population. If the latter interpretation is correct, the discrepancy can be equated with those found in the northern and southern study areas, and can be considered as fluctuations, temporary, chance phenomena. Rowell (1969) also recorded fluctuations around the norm in Papio anubis' sex ratio and emphasized the importance of seeing group composition as a dynamic process.

The causes of the "aberrant" ratios at Berenty in 1963/1964 remain obscure. It is possible that a disease differentially affecting females at some stage in their development decimated the female population of the reserve in earlier years. It is possible that there had been an influx of males into the reserve from surrounding areas in the process of being felled: there is some evidence that females are less likely to leave familiar areas than are males (see Pp. 64-72). However, these ideas are necessarily too speculative to warrant further discussion.

It has been suggested that Lemur macaco macaco populations also contain an excess of males (Petter, 1962a; Basilewsky, 1965; Jolly, 1966). The evidence comes from censuses made by Petter in a total period of eight weeks, spread out over one year, and from brief censuses made by Jolly. Further investigation is needed to establish whether these results really do represent a consistent excess of males. It is possible that, as was apparently the case with P. verreauxi, the populations sampled were aberrant, or that results were biased by a differential flight response between the

two sexes or by inadvertently sampling only the periphery of a population. Peripheralization of males and the formation of all-male groups has been noted in several primate species (Charles-Dominique, 1972; Martin, 1972; Crook, 1966; Stoltz and Saayman, 1970; Jay, 1965; Manley, pers. comm.) and could, if it occurs in L. m. macaco, have had profound effects on the small samples made to date.

SUMMARY

1) A census of group size and composition was made on ten groups of P. verreauxi at Berenty. This was the fourth census to be made on this population in eight years. Less extensive surveys were also made in two study areas and in forests at Ejeda and Evasy. Information on the processes of change in group composition came almost exclusively from the four study groups.

2) Only if on three separate occasions the same number of animals were counted in a group is that group included in the results. This, perhaps wrongly, assumes that apparent changes in group size were due to observer error rather than to real changes within the group.

3) Group size ranged from 3 - 10 in the five areas sampled, and mean group size varied from 5.0 - 7.0 between these areas. However, group size did not vary significantly between areas; this may be partly a function of the restricted sample sizes.

4) Births occurred in June and July in the northern study area, in 1970. The infant mortality rate for 1970/1971 was about 84% (n=6). Births in the south probably took place in early August, and the infant mortality rate there for 1970/1971 was 100% (n=4). No evidence for twinning was found. Four females gave birth in both 1970 and 1971. Combining Jolly's (1972) census at Berenty with that made in 1971, a 40% infant mortality rate can be inferred in these years (n=10).

5) One birth was witnessed. Fifteen minutes after the birth, the mother moved off with the infant clinging, unsupported, to her ventral surface. The mother ate the afterbirth. Other group members did not appear to pay any attention to the birth, or to the newly born infant.

6) P. verreauxi possesses a strident alarm call. In the course of the study, this was emitted in response to aerial raptors, man, a snake eating an adult Microcebus murinus, and to the sound of distant lorries. However, the existence of this call cannot be taken as firm evidence of predation pressure.

7) Aerial raptors, constrictor snakes and Cryptoprocta ferox may prey upon P. verreauxi, although no direct evidence for this was collected. The most important single predator of adult P. verreauxi is man. When stalked to within a few metres, however, groups may attack rather than flee.

8) A 3 - 4 year old female was found dying in the northern study area. Subsequent analysis revealed an infestation of non-pathogenic protozoans, but did not show the exact cause of death.

9) Deaths may also occur as a result of fighting during the mating season.

10) Males changed groups both in and out of the mating season. Changes in the mating season were accompanied by fierce fights, but during the rest of the year apparently took place peacefully.

11) Group size and age/sex composition at Berenty in 1971 differed little from the previous year, although in most cases the evidence did not demonstrate whether the actual identity of animals comprising groups remained the same.

12) P. verreauxi live in small units of highly variable composition. It would be inappropriate to categorize them as "family groups" or as "age-graded-male troops." Groups should be considered as foraging parties of mutually familiar animals rather than as reproductive units.

13) The information provided by this study suggests that the socionomic

sex ratio of P. verreauxi fluctuates about a norm of 1:1, and that the ratios recorded at Berenty in 1963/1964 were aberrant. The causes of those "abnormal" ratios remain obscure.

14) Limited evidence suggests that L. m. macaco populations have an excess of males. Further investigation is needed to establish whether this is another case of the population sampled being aberrant, or the results biased due to some other cause.

SECTION II: DESCRIPTION AND ANALYSIS OF THE STRUCTURE AND COMPOSITION OF THE FOREST IN EACH STUDY AREA

INTRODUCTION

A general description of the mixed deciduous forest of the northern study area and of the xerophytic, Didierea-dominated forest in the south has been given in Part IB. That description is expanded here on the basis of a vegetational analysis undertaken in both study areas.

The purpose of this aspect of the study was to provide detailed information on vegetation that might be useful in understanding seasonal and spatial variation in the ranging behaviour of the P. verreauxi groups studied.

The analysis presented here includes estimates of the height, density, diversity and distribution of tree species in each study area, and of the synchrony in leaf and fruit production between and within species.

METHODS

Sample size

A total of 2,619 trees were described in the northern study area, taken from 24 samples. In the south, 3,136 trees coming from 30 samples were described. In both areas, lianas constituted an important item in the diet of P. verreauxi. It was not possible to make an accurate estimate of the density of lianas, but a count was made of the number of trees bearing lianas in each sample in order to provide a rough estimate of abundance.

The size of the sample made in the two study areas was largely determined by practical considerations. The description, identification and frequent collection of fruit and leaves of tree species was a slow, laborious process.

Fig. 3. Map of northern study area showing grid system, approximate home-ranges of study groups, and location of vegetational samples.

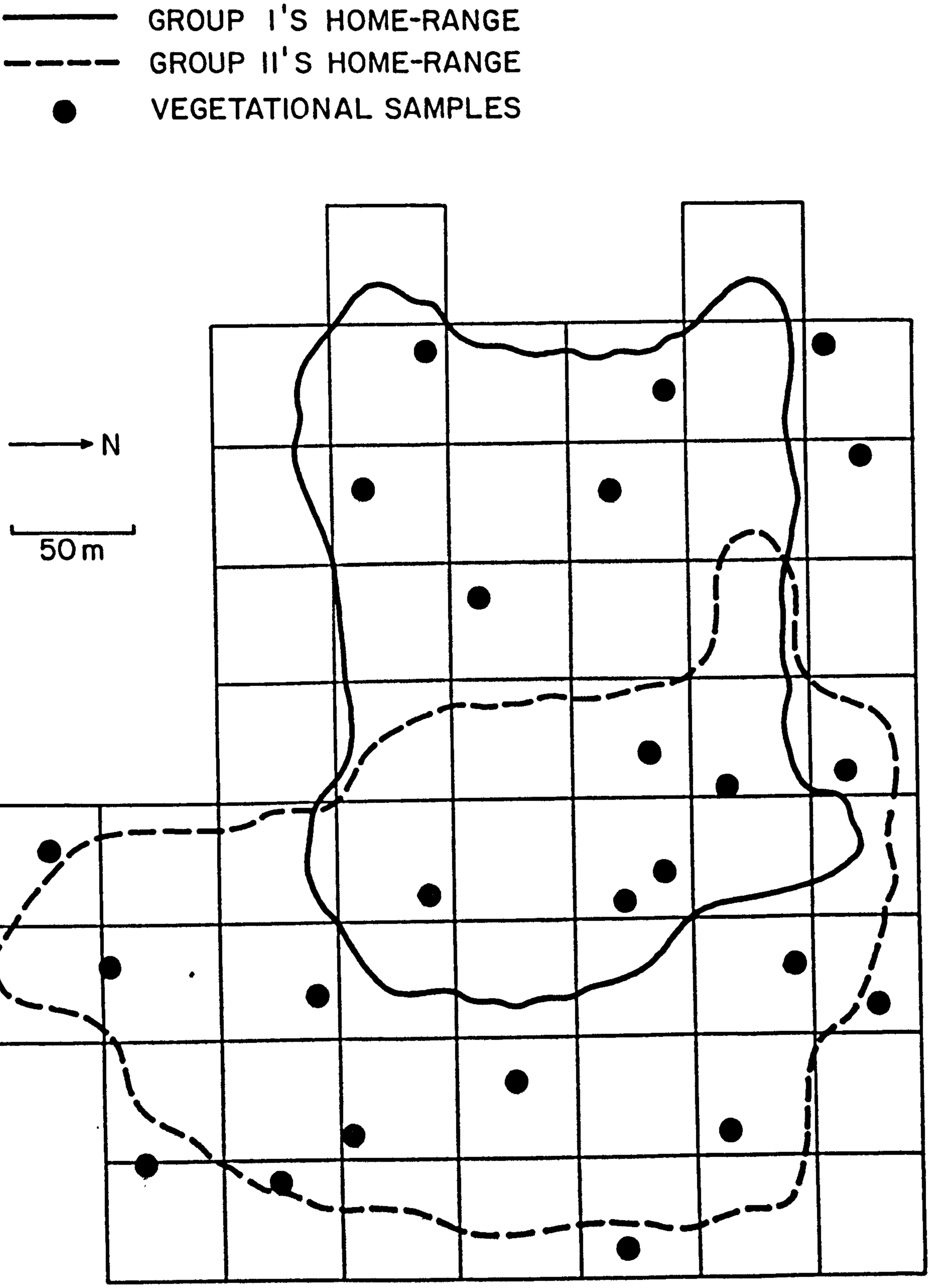
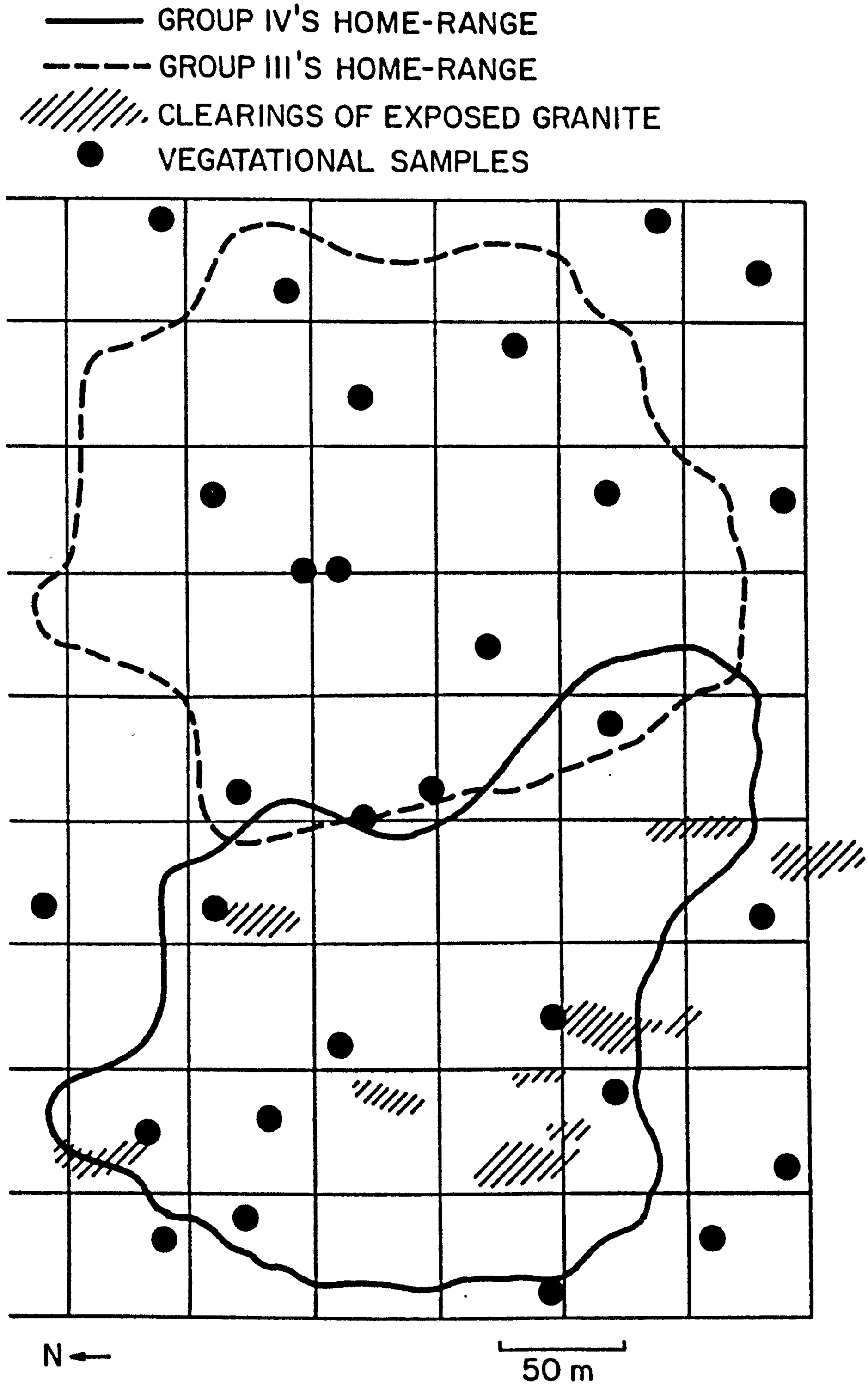

GROUP I'S HOME-RANGE
GROUP II'S HOME-RANGE
VEGETATIONAL SAMPLES
N
50 m

Fig. 4. Map of southern study area showing grid system, approximate home-ranges of study groups, location of vegetational samples, and location of exposed granite clearings.


GROUP IV'S HOME-RANGE
GROUP III'S HOME-RANGE
CLEARINGS OF EXPOSED GRANITE
VEGATATIONAL SAMPLES
N
50 m

Sample size was thus limited by the time available after the monthly collection of data on the study groups. Optimally, a wider, more meaningful sample would have been made, but in this field study the collection of such a sample would have reduced data collection on the animals to a minimum. This in turn would have defeated the purpose of the sample.

Distribution of samples

In each study area, the total area from which samples were taken extended slightly beyond the home ranges of the two study groups. This was because the whole squares of the grid which were only partially occupied on the periphery of home-ranges were included in the analysis (see Figures 3 and 4). Two samples were made in each hectare square delineated by the grid system, so that by the end of the anlaysis trees growing in 1.57% of each study area had been analysed.

Within each square hectare the two samples were randomly located. The location of the samples was determined by considering the sides of each hectare square as axes and using a table of random numbers to plot coordinates. Samples were taken at the resulting point, which was paced out in the field. This general method followed the "stratified random" sample technique described by Southwood (1966). It ensured that the total sample was well distributed over the total area to be sampled. At the same time, the bias that might arise if species distributed in a uniform pattern were also sampled according to a uniform pattern was minimized by randomization within each hectare square. The location of these samples is shown on Figures 3 and 4. Fewer samples were necessary in the north because the extensive home-range overlap between the two study groups reduced the total area to be sampled (see Section III).

Method of sampling

Each sample consisted of a circle with a measured radius of 5m. Within each circle, all trees with a trunk diameter greater than 3cm. at chest level were counted, and the trunk diameter, height and maximum spread, height of the lowest branch above the ground and phenology were noted for each tree. The low minimum trunk diameter of 3cm. was selected because of the large number of small trees with thin trunks in both areas that played an important role in the diet of P. verreauxi. Where possible, samples of leaves, flowers and fruit were collected for subsequent identification.

Estimating tree height and spread

Tree height, maximum spread, and the height of the lowest branch above the ground were estimated by eye. A spot check was subsequently made on 200 trees whose height had already been estimated at 15m. or less: their height was more accurately measured by climbing to the top of them and letting down a 15m. rope. Similarly, the spread was measured by stretching this rope across the ground under each tree from one extremity to the other. In all cases estimates by eye were accurate to within ±2m. of the measured distances, and in 117 cases to within ±1m. These methods might be inappropriate in high stature forest, for the accurate estimation of tree height by eye alone becomes increasingly difficult as that height increases. In addition, the crude techniques for checking estimates described above would not be practical. However, in the dense, low stature forests of the present study (see P.99) the system was practical and within the general limits of accuracy of the study. In the analysis below, tree heights have been grouped after Jolly (1966) in order to facilitate comparison. Her system grouped all trees over 21m. high which, in this study, minimizes the effect of any inaccuracy in estimates of the height of taller trees.

Assessing synchrony in phenology

Data on synchrony of leaf and fruit production and their presence in tree species were based on observations made on ten species in each study area. Some of these species were selected because they constituted a large proportion of P. verreauxi's diet during the first month of observation in each study area, and others because they were abundant in each forest and hence might be important in the animals' diet in other seasons.

Each month, observations on ten individual trees from each species were tabulated, taken from the main vegetational samples where possible. Different individual trees were used each month in order to ensure independence of the data. Five generalized categories were used to describe the condition of these trees:

1) leaf shoots and/or young leaves and flush. (Young leaves were differentiated from adult leaves on the basis of their paler colouring and, sometimes, smaller size.)
2) adult and/or dying leaves
3) flowers in bud and/or blossom
4) fruit, green and/or ripe
5) dormant buds

Evidently, these categories are not mutually exclusive. Initial attempts to subdivide them further were abandoned when it proved impossible to find a consistent, clear-cut operational definition of each state that would be equally applicable to all species.

RESULTS

Density of trees

Mean density of trees in the two study areas was closely comparable: 109 per circle sampled in the north, and 105 in the south. Extrapolating

from these figures, the estimated density of trees per hectare was 13,878 in the north and 13,370 in the south.

The similarity between the two study areas suggested by the estimated density of trees is misleading: there were several important differences in the structure of the vegetation.

1) Ground layer. The proliferation of tough woody lianas and shrubs in the north made the forest impenetrable to P. verreauxi and myself alike at ground level in some parts. In the south, the forest floor was generally covered by moss-like Selaginella species, and scattered with small woody shrubs. Rarely more than 1 m. in height and usually growing singly or in small clumps, these shrubs provided no effective barrier to progressions on the ground.

2) Foliage. Both the abundance and size of leaves was much greater in the north than in the south. The general reduction of foliage in the south may be an adaptive response to arid conditions: botanical studies carried out in other xerophytic forests endorse this idea. Plants may adapt to chronic water shortage in many ways, including extreme reduction or even disappearance of leaves (Schimper, 1903; Kearney and Shantz, 1911; Oppenheimer, 1960; Treshow, 1970).

Data collected on the height and maximum spread of sampled trees (see P. 99) and on the frequency of occurrence of lianas, give some indication of the great abundance of foliage in the north. Lianas grew on a mean of 70% of the trees sampled per circle in the north. This was significantly more than in the south, where they grew on a mean of only 30% of the trees sampled per circle (t test, $t=9$, $N=48$, $p \leq .01$).

Clutton-Brock (in press) estimated the surface area of the foliage of trees. He estimated the maximum spread of foliage, and its height (the distance between the top of the tree and the branch closest to the ground). He then calculated surface area on the assumption that the tree had the approxi-

Fig. 5. Variation in density of trees between vegetational samples, within each study area.

Fig. 6. Distribution of sampled trees between height categories, within each study area.

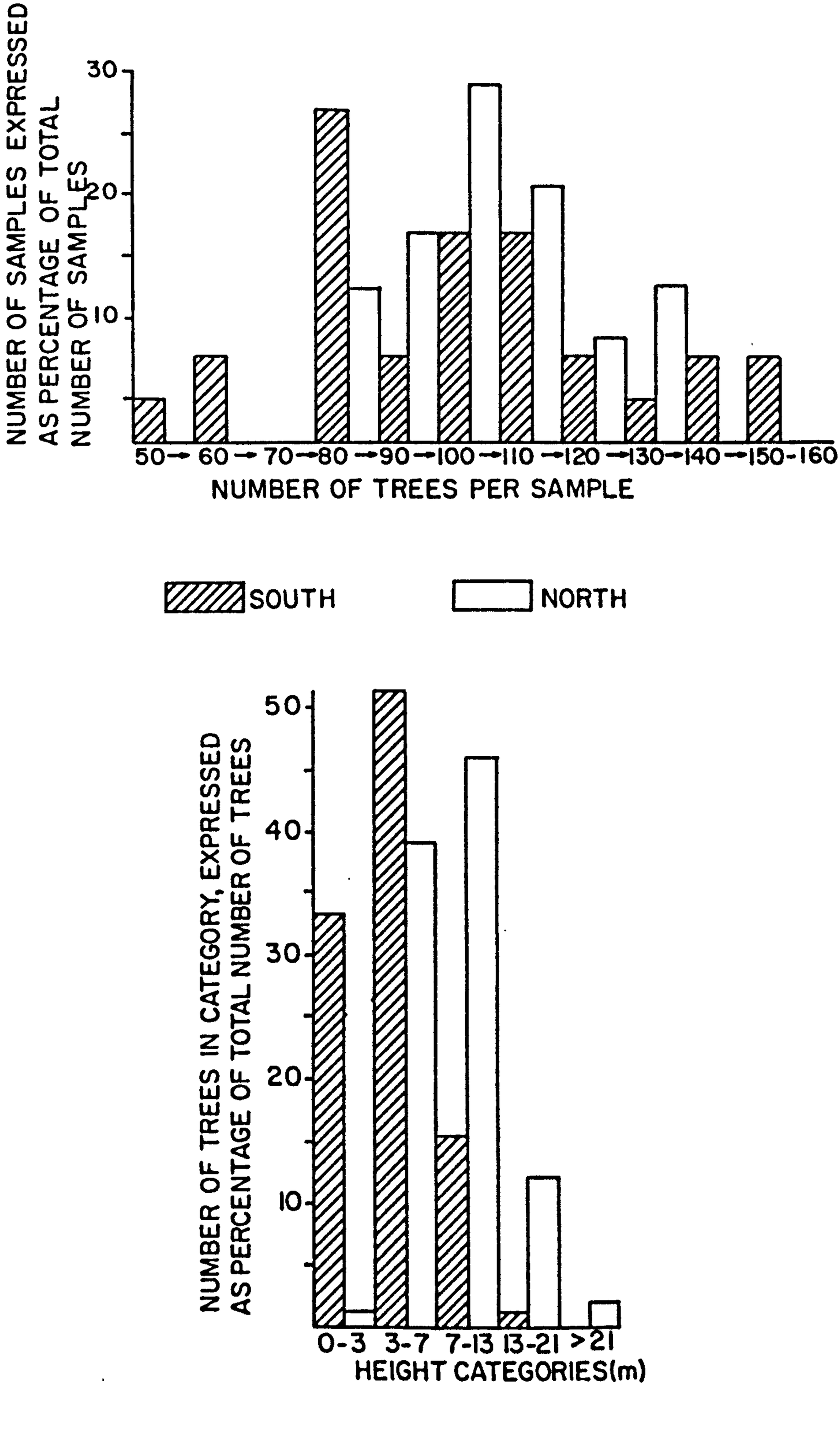

NUMBER OF SAMPLES EXPRESSED AS PERCENTAGE OF TOTAL NUMBER OF SAMPLES
30
20
10
50→ 60→ 70→80→90→100→110→120→130→140→150-160
NUMBER OF TREES PER SAMPLE
SOUTH
NORTH
NUMBER OF TREES IN CATEGORY, EXPRESSED AS PERCENTAGE OF TOTAL NUMBER OF TREES
50
40
30
20
10
0-3 3-7 7-13 13-21 >21
HEIGHT CATEGORIES(m)

TABLE 4: Tree species collected in the course of the vegetational analysis in the northern study area, giving scientific names where known, the total number of individuals of each species counted, and the number of sample circles in which they were found (Total number of sample circles = 24).

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
Euphorbiaceae	Drypetes sp. No. 18	323	24
Oleaceae	Noronhia sp. No. 93	208	24
Rhizophoraceae	Cassipourea sp. No. 179	116	13
Rhopalocarpaceae	Rhopalocarpus similis Hemsley	103	24
Acanthaceae	No. 111	103	23
	Rothmannia decaryi	85	19
Sapotaceae	Capurodendron microlobum (Baker) Aubreville	78	21
Leguminosae	Baudouinia fluggeiformis Baill.	71	22
Anacardiaceae	Protorhus deflexa H. Perr	67	19
Tiliaceae	Grewia sp. No. 121	57	20
Euphobiaceae	Alchornea alnifolia	56	17
Oleaceae	Anacolosa pervilleana Baill.	56	21
Meliaceae	Cedrelopsis sp. No. 123	54	10
Burseraceae	Commiphora pervilleana	51	16
Myrtaceae	Eugenia tropophylla H. Perr	50	6
Guttiferae	Rheedia arenicola Jerm Perr	43	14
Ebenaceae	Diospyros sp. No. 126	41	5

TABLE 4: Cont.

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
Guttiferae	Mammea sp. No. 5	36	14
Anacardiaceae	Poupartia sp. No. 244	34	6
Apocynaceae	Hazunta sp. No. 156	33	15
Rubaceae	No. 276	32	11
Rhizophoraceae	Cassipourea sp. No. 155	31	10
Meliaceae	Astrotrichilia sp. No. 25	26	15
Sapindaceae	Macphersonia gracilis D. Hof.	25	10
Sapotaceae	Mimusops sp. No. 320	24	8
Oleaceae	Linociera tropophylla H. Perr	23	13
Euphorbiacae	Euphorbia sp. No. 89	21	12
Ebenaceae	Diospyros sp. No. 118	20	15
Annonaceae	Polyalthia Henricii Diels	19	8
Rutaceae	Vepris sp. No. 221	17	8
Canellaceae	Cinnamosma fragrans Baill.	17	10
Ochnaceae	No. 341	16	9
Celastraceae	Mystroxylon aethiopium	16	12
Sterculiaceae	Nesogordonia stylosa H. Perr	16	10
Capparidaceae	Boscia sp. No. 301	15	6
Verbenaceae	Premna longiacuminata	15	9
Papilionaceae	Dalbergia sp. No. 544	14	6
	No. 173	13	10

TABLE 4: Cont.

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
Papilionaceae	Mundulea sp. No. 64	13	6
	Bathiorhamnus louveli (H. Perr) R. Cap. ssp. reticulatus R. Cap.	12	7
Euphorbiaceae	Phyllanthus sp. No. 113	12	4
	Mallaeastrum sp. No. 240	9	6
Myrtaceae	Eugenia sp. No. 348	9	5
Boraginaceae	Vitex bereviensis	9	8
Meliaceae	Cedrelopsis sp. No. 471	8	6
Rubiaceae	Canthium sp. No. 630	8	3
Myrsinaceae	Ardisia didymopora (Perr) R. Cap.	8	6
	No. 269	8	2
	No. 433	7	2
Myrtaceae	Eugenia sp. No. 603	7	3
	No. 358	7	4
Papilionaceae	Indigofera sp. No. 1	7	4
Boraginaceae	Vitex sp. No. 80	7	7
Ochnaceae	No. 97	7	7
Loganiaceae	Strychnos madagascariensis	7	6
	No. 183	7	2
Rubiaceae	Enterospermum sp. No. 81	6	9
	Holmskioldia microcalyx (J. F. Baker) Pieper	6	5

TABLE 4: Cont.

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
Loganiaceae	Strychnos sp. No. 142	6	4
	No. 336	6	5
Guttiferae	Psorospermum cerasifolium Baill.	10	6
	No. 260	6	2
	No. 339	6	1
	No. 492	6	3
Euphorbiaceae	Sapium melanostictum	5	5
Tiliaceae	Grewia sp. No. 387	5	3
Erythroxylaceae	Erythroxylon sp. No. 530	7	5
	No. 582	5	3
Sapindaceae	Allophylus cobbe 'saligna'	5	2
Tiliaceae	Grewia picta Baill.	5	2
Meliaceae	Cedrelopsis grevei Baill.	4	4
	No. 73	4	1
Mimosaceae	Albizzia arenicola R. Viguier	4	3
	No. 229	4	2
Capparidaceae	Boscia sp. No. 403	4	2
	No. 511	4	1
Loganiaceae	Strychnos decussata Gilz.	3	2
Verbenaceae	Premna perplexans Mold.	3	1

TABLE 4: Cont.

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
Euphorbiaceae	Securinega seyrigii Leandri	3	1
	Malhestrum aubingyense	3	3
	No. 192	3	3
	No. 331	3	2
	No. 509	3	1
	No. 586	3	1
	No. 607	3	1
	No. 623	3	1
	No. 615	3	2
	No. 614	2	1
	No. 618	2	1
	No. 619	2	1
	No. 344	2	1
	No. 600	2	2
Erythroxylaceae	Erythroxylon sp. Sp. No. 514	2	2
Pedaliaceae	Uncarina sp. No. 543	2	1
Capparidaceae	Boscia sp. No. 601	2	2
Annonaceae	No. 239	2	2
Rutaceae	Vepris sp. No. 263	2	1
Chrysobalanaceae	Grangeria porosa Boiv. ex Baill.	2	1
Sarcolaenaceae	Perrierodendron boineuse (Perr) Cav.	2	2

TABLE 4: Cont.

Family	Genus & Species and/or given number	Total Number Found	Number of sample circles in which species was found
	No. 171	2	1
Capparidaceae	Boscia sp. No. 69	2	1
Sapindaceae	Allophylus sp. No. 127	2	1
Compositae	Brachylaena sp. No. 165	2	2
Rutaceae	Vepris sp. No. 178	2	2
Rubiaceae	Gardenia suavissima Hom. ex Cavaco	2	2

One tree of each of the following species was noted:- Acanthaceae fam., No. 29; Rhizophoraceae Cassipourea sp. No. 46; Ebenaceae Diospyros sp. No. 169; Sapindaceae Allophylus cobbe 'salicifolia; Rhamnaceae Ziziphus mauritiana Lamk; Meliaceae fam., No. 316; Euphorbiaceae Drypetes sp. No. 435; Humbertioturraceae fam., No. 411; Annonaceae Xylopia sericolampra (Dicks); Erythroxylaceae Erythroxylon sp. No. 469; Phyllarthron bernierianum; Euphorbiaceae Croton sp. No. 569; Combretaceae Terminalia bovinii Tul.; Ardesia sp. No. 590; Burseraceae Commiphora sp. No. 591; Canthium sp. No. 592; Rhamnaceae Berchemia discolor; Combretaceae Terminalia tropophylla Perrier; Humbertioturraceae Humbertioturrea sp. No. 620; Linaceae Hugonia longipes H. Perr; Ebenaceae Diospyros sp. No. 405; Meliaceae Turraea sp. No. 558; and Spp. nos. 66, 107, 101, 75, 78, 138, 170, 144, 186, 191, 602, 248, 261, 232, 233, 322, 330, 334, 335, 336, 425, 45, 485, 486, 487, 483, 488, 489, 493, 504, 516, 517, 588, 585, 587, 596, 597, 599, 606.

A further 213 trees, spread over 23 sample circles, were found with dormant buds only, and could not be distinguished individually, so that no number could be given to them.

TABLE 5: Tree species collected in the course of the vegetational analysis in the southern study area, giving scientific names where known, the total number of individuals of each species counted, and the number of sample circles in which they were found. (Total number of sample circles = 30.)

Family	Species & Genus and/or given number	Total number found	Number of sample circles in which species was found
Didieriaceae	Alluaudia procera	916	30
Burseraceae	Commiphora humbertii H. Perr	607	29
Didieriaceae	Alluaudia ascendens	251	24
Meliaceae	Cedrelopsis grevei Baill.	211	23
Combretaceae	Terminalia sp. No. 048	132	27
Buseraceae	Commiphora orbicularis Engler	117	22
Euphorbiaceae	Euphorbia plagiantha	115	10
Burseraceae	Commiphora sp. No. 076	72	21
Ebenaceae	Diospyros humbertiana H. Perr	66	13
Burseraceae	Commiphora simplicifolia H. Perr	66	23
Anacardiaceae	Operculicarya decaryi H. Perr	56	23
Euphorbiaceae	Securinega sp. No. 016	50	13
Tiliaceae	Grewia sp. No. 089	35	16
Hernandiaceae	Gynocarpus americanus Jacq.	34	11
	No. 015	27	17
Euphorbiaceae	No. 080	27	11
Euphorbiaceae	No. 098	25	10
Didieriaceae	Alluaudia humbertii	21	6
Mimosaceae	Mimosa sp. No. 033	21	9

TABLE 5: Cont.

Family	Species & Genus and/or given number	Total number found	Number of sample circles in which species was found
Cesalpinia	Tetrapterocarpum geayi H. Humb.	20	11
Burseraceae	Hymenodictyon sp. No. 075	19	15
Combretaceae	Terminalia sp. No. 0109	19	5
Euphorbiaceae	Croton sp. No. 062	18	8
Rubiaceae	Enterospermum sp. No. 085	18	13
Apocynaceae	Hazunta modesta (Bak.) M. Pichon	17	9
Combretaceae	Terminalia sp. No. 09	16	8
Tiliaceae	Grewia sp. No. 059	14	7
Tiliaceae	Grewia sp. No. 0106	14	5
Bignoniaceae	Stereospermum nematocarpum	11	6
Leguminaceae	No. 051	11	2
Meliaceae	Neobeguea mahafalensis J. Leroy	10	8
Bignoniaceae	Rhigozum madagascariense Drake	10	4
Ebenaceae	Diospyros sp. No. 013	9	6
Euphorbiaceae		9	4
Salvadoraceae	Salvadora angustifolia Turill.	8	5
	No. 099	8	7
Burseraceae	Commiphora sp. No. 092	6	5
Cesalpinia	Baudouinia fluggeiformis	5	3

TABLE 5: Cont.

Family	Species & Genus and/or given number	Total number found	Number of sample circles in which species was found
Tiliaceae	Grewia sp. No. 0126	5	2
	No. 026	5	1
Burseraceae	Hymenodictyon sp. No. 093	4	4
Burseraceae	Commiphora brevicalyx H. Perr	3	3
	No. 0100	3	1
Papilionaceae	Indigofera sp. No. 0111	3	1
	No. 0121	3	1
	No. 095	3	1
Mimosaceae	Albizzia sp. No. 084	2	1
Bombacaceae	Adansonia fony	2	2
Malvaceae	Hibiscus sp. No. 0116	2	2
Apocynaceae	Pachypodium Lamerei Drake	2	2
Mimosaceae	Entada abyssinica Stendel	2	2
Rubiaceae	Enterospermum sp. No. 0120	2	2
	No. 0130	2	1
Capparidaceae	Boscia longifolia Hadj. Monst.	2	2
Apocynaceae	Rauwolfia confertiflora M. Pichon	2	2
Urticaceae	Pouzolzia gaudichaudii J. Léandri	2	2

TABLE 5: Cont.

One tree of each of the following species was noted: Verbenaceae Vitex microphylla Moldenke; Euphorbiaceae Croton sp. No. 067; Euphorbiaceae Croton sp. No. 083; Diospyros sp. No. 0108; Acacia sp. No. 0110; Croton sp. No. 0123; Stereospermum sp. No. 0143; Rothmannia decaryi, Rhus thouarsii H. Perr; Albizzia sp. No. 084; and spp: nos. 097, 0113, 0134, 0142.

mate shape of a cylinder open at one end. No such estimate was made in the present study because the extensive variation in tree shape within each area and, particularly, between each area, made it impossible to provide a formula measuring surface area that would be universally applicable.

3) Variation in density. The figures for mean density of trees per unit area do not indicate the range of variation in density between sample circles. Figure 5 shows that the range was greater in the south (F=2.78, N=54, $p \leq .01$). The significance of this difference was partly produced by samples in the south that included expanses of exposed rock. There were nine of them in the southern study area ranging from approximately 0.025ha. to 0.25ha. in size. Their location is shown in Figure 4. Such clearings did not exist in the northern study area. When sample circles that included clearings are excluded from calculations, no significant difference remains in the range of variation of density between north and south.

Tree height and spread

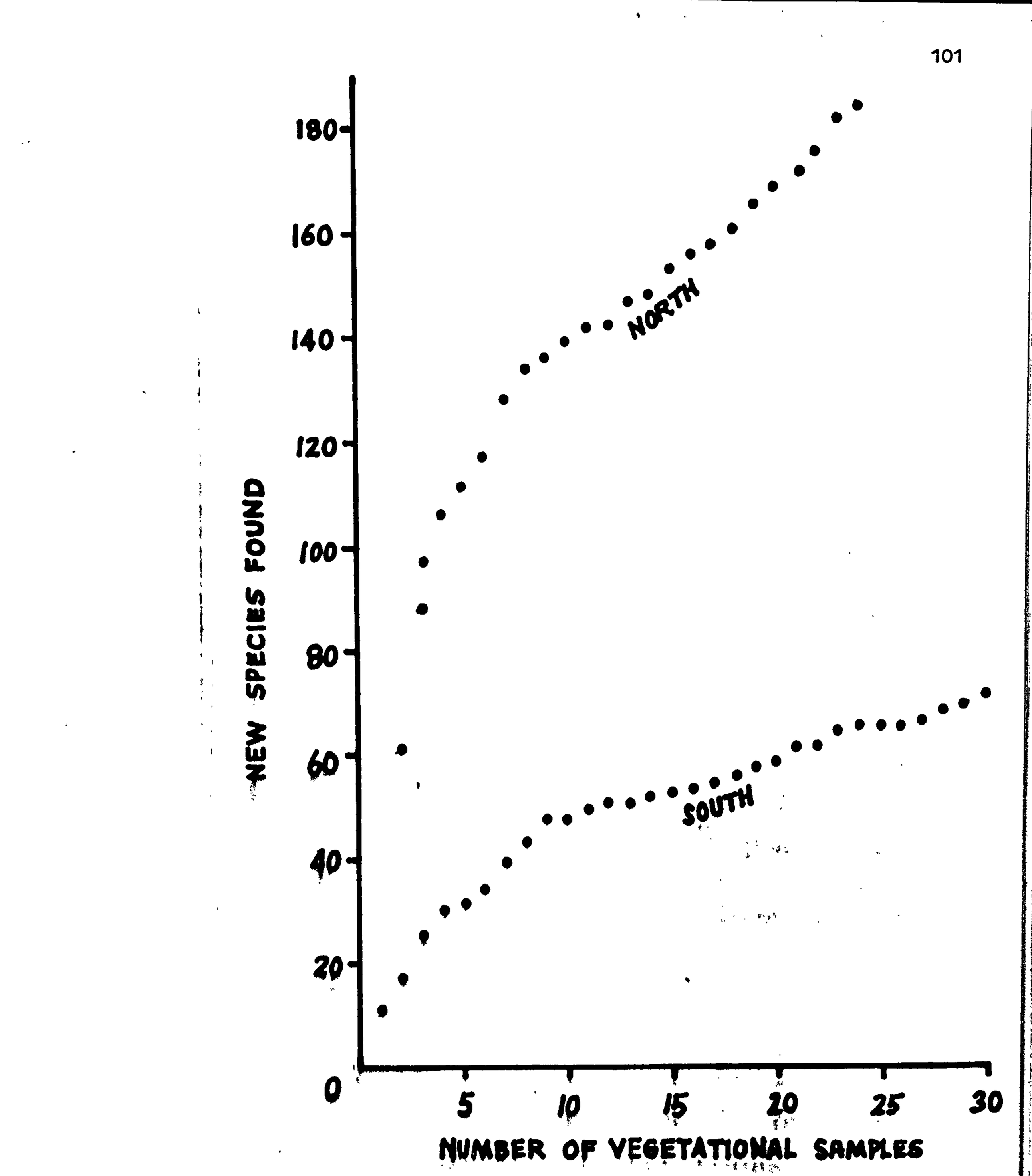
The distribution of trees between the various height categories (see Figure 6) shows that there were more trees of greater stature in the north than in the south (Kolmogorov-Smirnov two-sample test, $n_1=2619$, $n_2=3136$, D=0.314, p=.001).

Summing the maximum spread of all trees in each circle, the mean summed spread of trees per circle in the north was 493.6m. That in the south was only 214.4m. The difference between these figures was highly significant (t test, N=54, t=10.6, $p \leq .001$).

Diversity and distribution of tree species

Tables 4 and 5 list the species collected during sampling in each study area, their total frequency, and the number of samples in which each species was found. Those that could not subsequently be identified are referred to

Fig. 7. Cumulative number of new tree species found in progressive samples during the analysis of vegetation in each study area.


NEW SPECIES FOUND
180
160
140
120
100
80
60
40
20
0
NORTH
SOUTH
5
10
15
20
25
30
NUMBER OF VEGETATIONAL SAMPLES

by a number. Many more species belonging to many more families were found in the north: at least 167 species, belonging to at least 35 families were collected. In the south, the equivalent figures were only 70 and 23.

Two points should be emphasized. First, for both areas sampled these figures probably underestimate the actual diversity of species. Tree species were seen which never fell within sample circles, and new species continued to be found throughout the analysis (see Figure 7). Thus, all figures quoted here should be considered as indicators of minimum values rather than absolutes.

Secondly, any measure of the range of species present relates to a specific area size and does not give an absolute estimate of the number of species in the whole forest. In this study, samples were taken from an area of about 14ha. in the north, and 13ha. in the south. In both forests, samples taken over a wider area would have revealed much greater diversity, as a function of progressive change in the composition of the vegetation which was, locally, relatively homogeneous. Vegetational change was associated with topographical change and hence probably with less obvious factors such as drainage, soil type, exposure to sun. For example, in the north, few species found in the hill-top study area were seen at the foot of the hill. In the south, a radical change in the composition of vegetation was apparent when I climbed hills surrounding the study area.

The mean number of species counted per sample in the north was 35 (range 28-41). In the south it was only 17 (range 10-25). The difference between these figures was highly significant (t test, N=54, t-16.8, $p \leq .001$). Figure 7 shows the cumulative number of <u>new</u> species found in progressive sample circles. In the north, over 50% of all species found, were represented in the first 16% of the total sample; in the south, over 50% were present in the first 20%. The rate at which "new" species were recorded subsequently decreased. Later records of "new" species could be the result of sampling

Fig. 8. Tree species grouped according to the number of sample circles in which each occurred, in each study area.

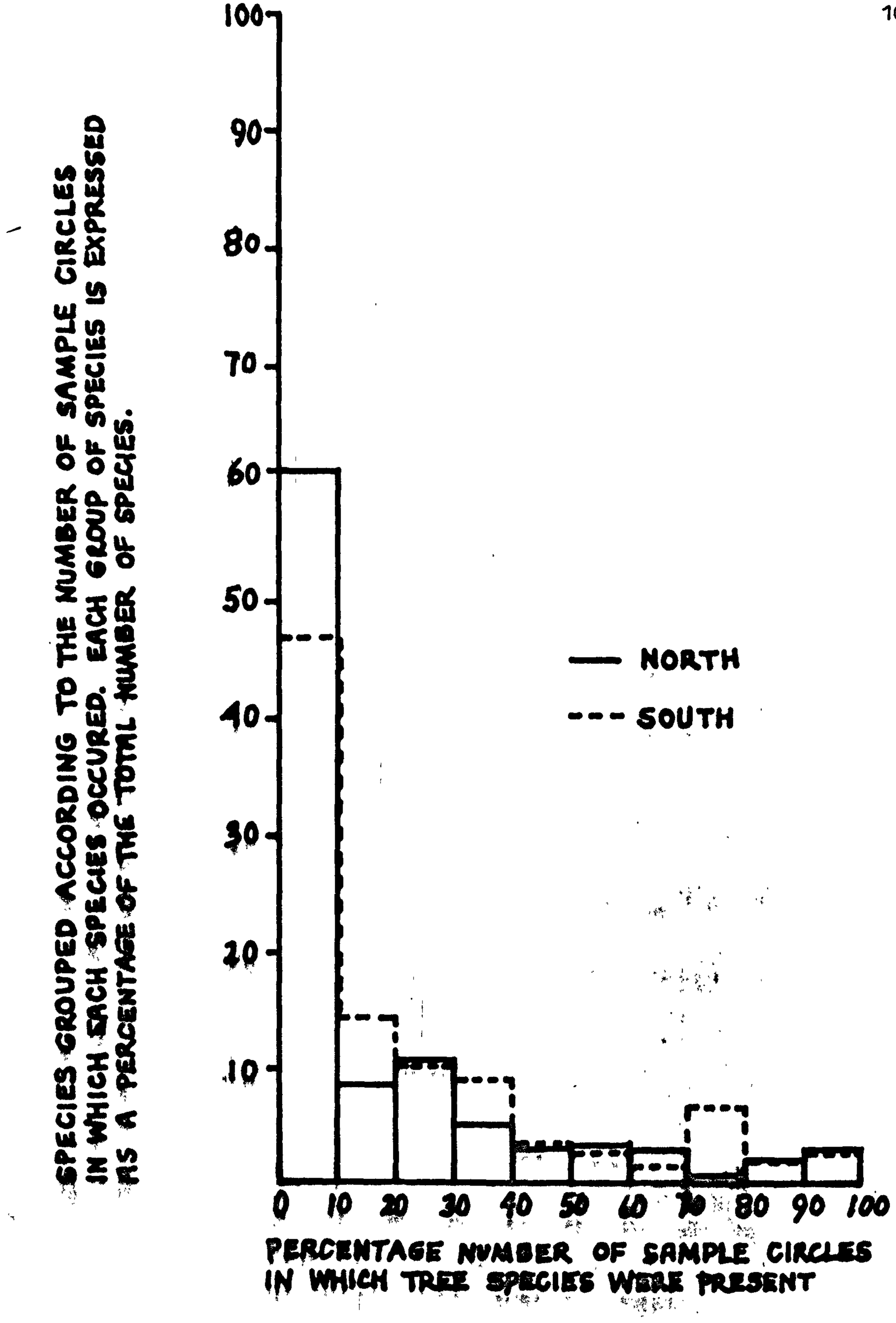

SPECIES GROUPED ACCORDING TO THE NUMBER OF SAMPLE CIRCLES IN WHICH EACH SPECIES OCCURED. EACH GROUP OF SPECIES IS EXPRESSED AS A PERCENTAGE OF THE TOTAL NUMBER OF SPECIES.
100
90
80
70
60
50
40
30
20
10
NORTH
SOUTH
0 10 20 30 40 50 60 70 80 90 100
PERCENTAGE NUMBER OF SAMPLE CIRCLES IN WHICH TREE SPECIES WERE PRESENT

Fig. 9. Phenology of trees sampled from ten species in the northern study area during the study period.

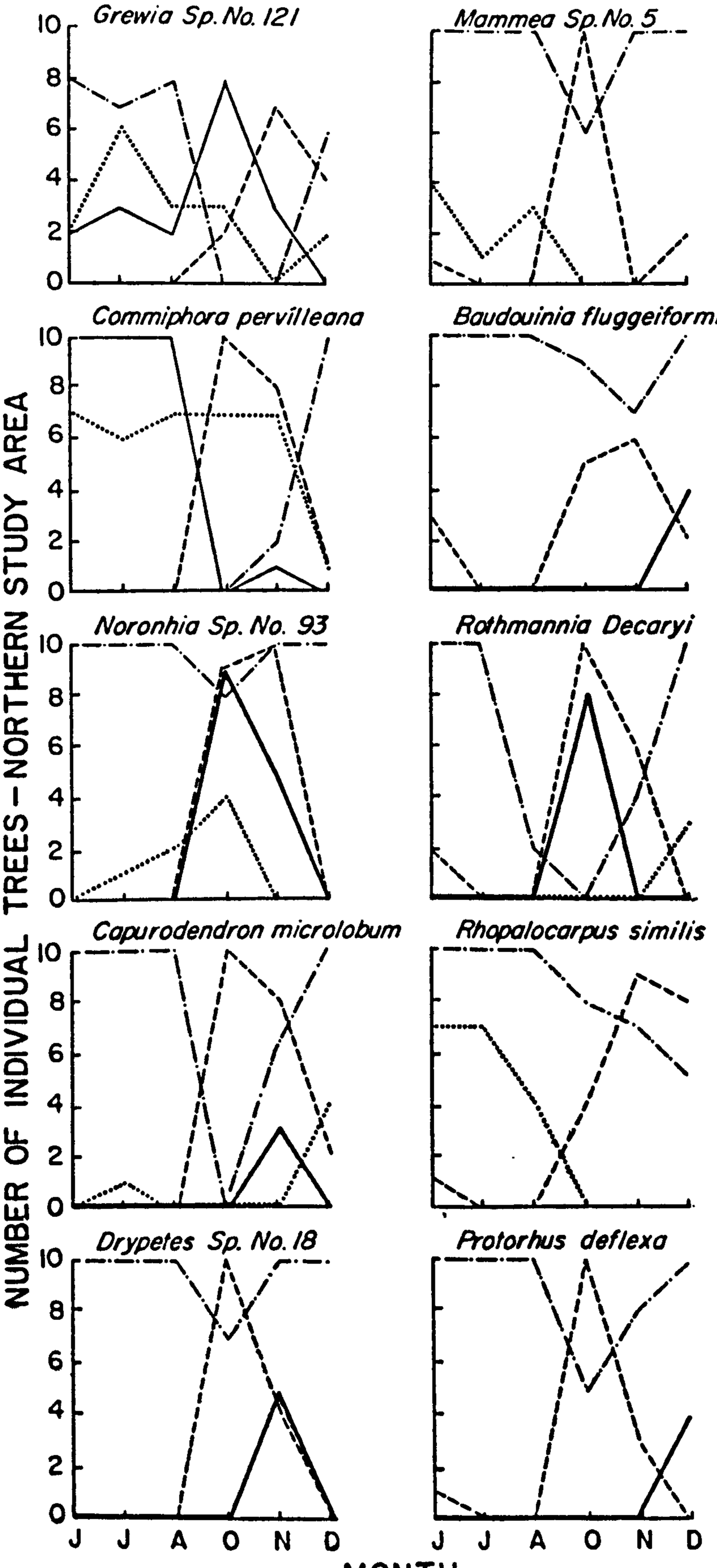

Grewia Sp. No. 121
Mammea Sp. No. 5
Commiphora pervilleana
Baudouinia fluggeiformis
Noronhia Sp. No. 93
Rothmannia Decaryi
Capurodendron microlobum
Rhopalocarpus similis
Drypetes Sp. No. 18
Protorhus deflexa
NUMBER OF INDIVIDUAL TREES – NORTHERN STUDY AREA
0
2
4
6
8
10
J J A O N D
MONTH
No leaves
Young leaves
Adult leaves
Flowers
Fruit

Fig. 10. Phenology of trees sampled from ten species in the southern study area during the study period.

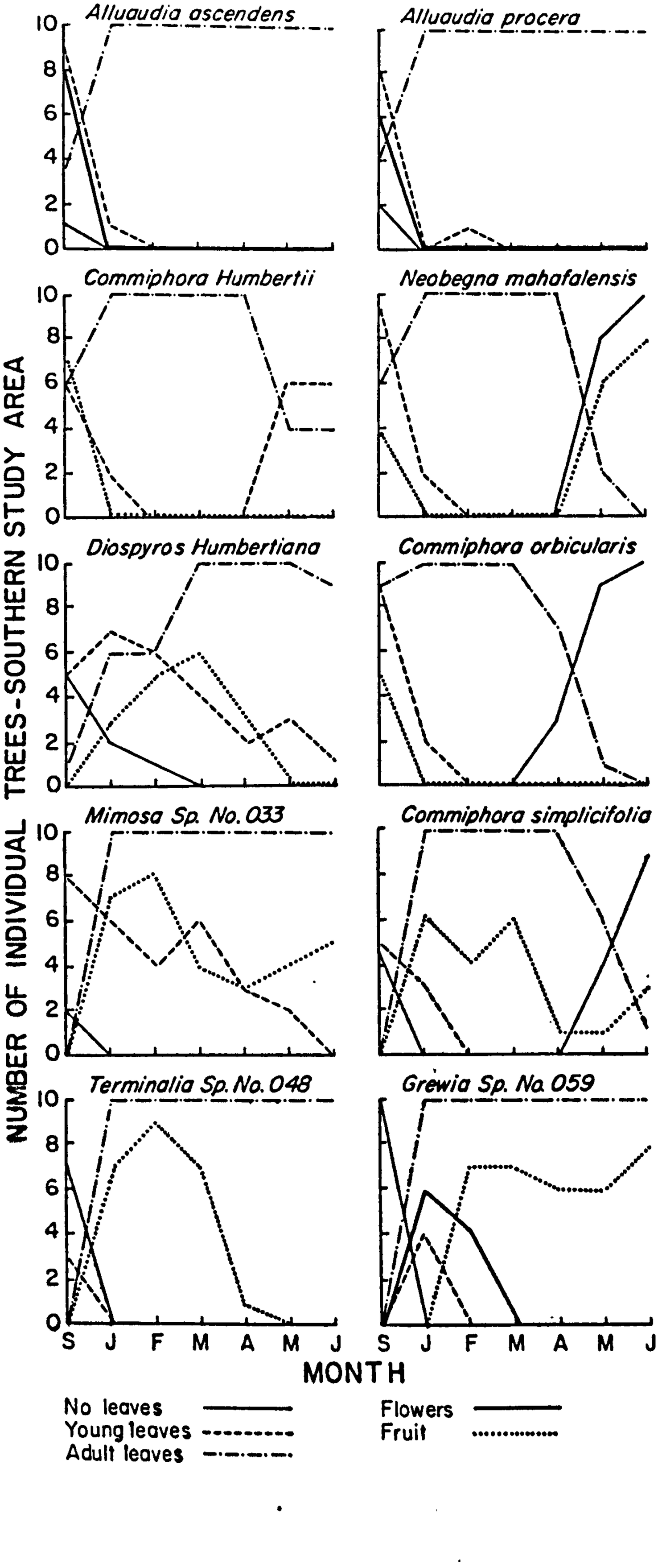

Alluaudia ascendens
Alluaudia procera
Commiphora Humbertii
Neobegna mahafalensis
Diospyros Humbertiana
Commiphora orbicularis
Mimosa Sp. No. 033
Commiphora simplicifolia
Terminalia Sp. No. 048
Grewia Sp. No. 059
TREES-SOUTHERN STUDY AREA
NUMBER OF INDIVIDUAL
0
2
4
6
8
10
S J F M A M J
MONTH
No leaves
Young leaves
Adult leaves
Flowers
Fruit

Fig. 11. Degree of synchrony among trees sampled from ten species in each study area.

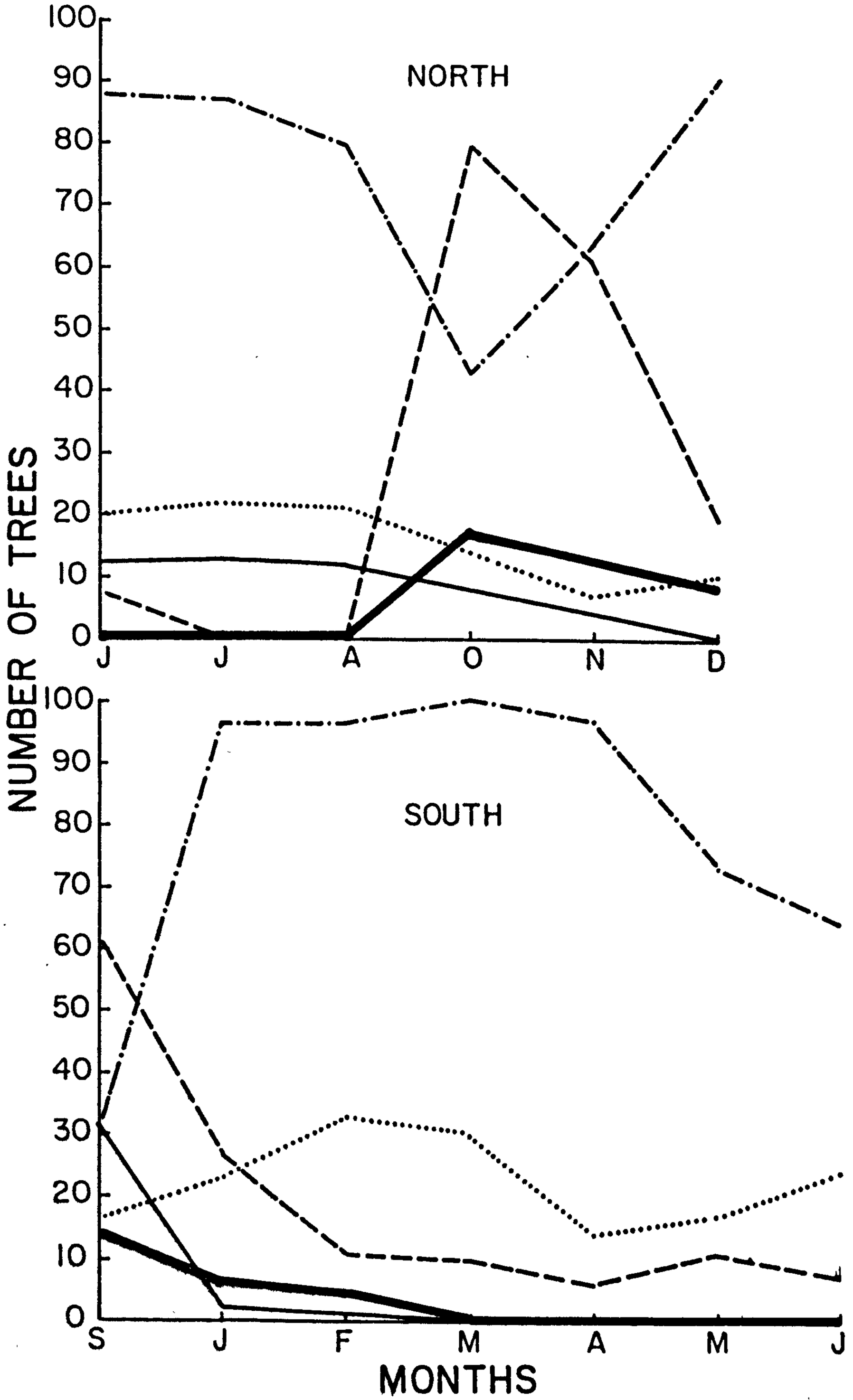

NORTH
100
90
80
70
60
50
40
30
20
10
0
J
J
A
O
N
D
NUMBER OF TREES
SOUTH
S
J
F
M
A
M
J
MONTHS
flowers
fruit
no leaves
young leaves
adult leaves

TABLE 6: Tree species grouped and ranked according to the number of sample circles in which they occurred.

NORTH

Number of species	Number of species expressed as a percentage of total number of species	Number of samples	Number of samples expressed as a percentage of total number of samples
3	1.8	24	100
1	.6	23	95.7
1	.6	22	91.5
2	1.2	21	87.4
1	.6	20	83.2
2	1.2	19	79.0
1	.6	17	70.7
1	.6	16	66.6
3	1.8	15	62.4
2	1.2	14	58.2
2	1.2	13	54.1
2	1.2	12	50.0
1	.6	11	45.8
5	3.0	10	41.6
3	1.8	9	37.4
4	2.4	8	33.3
6	3.6	7	29.1
10	6.0	6	25.0
5	3.0	5	20.8
5	3.0	4	16.6
8	4.8	3	12.5
19	11.4	2	8.3
80	47.8	1	4.7

TABLE 6: Cont.

SOUTH

Number of species	Number of species expressed as a percentage of total number of species	Number of samples	Number of samples expressed as a percentage of total number of samples
1	1.4	30	100
1	1.4	29	96.6
1	1.4	27	89.9
1	1.4	24	79.9
3	4.3	23	76.6
1	1.4	22	73.3
1	1.4	21	69.9
1	1.4	17	56.6
1	1.4	16	53.3
1	1.4	15	50.0
3	4.3	13	43.3
3	4.3	11	36.6
2	2.8	10	33.3
2	2.8	9	30.0
3	4.3	8	26.6
2	2.8	7	23.3
3	4.3	6	20.0
4	5.7	5	16.6
3	4.3	4	13.3
2	2.8	3	10.0
10	14.3	2	6.7
21	30.0	1	3.3

TABLE 6: Cont.

SOUTH

Number of species	Number of species expressed as a percentage of total number of species	Number of samples	Number of samples expressed as a percentage of total number of samples
1	1.4	30	100
1	1.4	29	96.6
1	1.4	27	89.9
1	1.4	24	79.9
3	4.3	23	76.6
1	1.4	22	73.3
1	1.4	21	69.9
1	1.4	17	56.6
1	1.4	16	53.3
1	1.4	15	50.0
3	4.3	13	43.3
3	4.3	11	36.6
2	2.8	10	33.3
2	2.8	9	30.0
3	4.3	8	26.6
2	2.8	7	23.3
3	4.3	6	20.0
4	5.7	5	16.6
3	4.3	4	13.3
2	2.8	3	10.0
10	14.3	2	6.7
21	30.0	1	3.3

TABLE 7: Degree of within-species synchrony of phenology in ten tree species in each study area

Sp.	Fruit	No Leaves	Adult leaves	Young leaves	Flowered	Total
North						
Grewia sp. No. 121	14	12	11	9	-	46
Mammea sp. No. 5	8	-	4	3	-	15
Commiphora pervilleana	17	1	2	3	-	23
Baudouinia fluggeiformis	-	-	4	14	4	22
Moronhia sp. No. 92	7	-	2	1	1	11
Rothmannia Decaryi	3	-	6	4	2	15
Capurodendron microlobum	5	-	4	4	3	16
Rhopalocarpus similis	10	-	10	8	-	28
Drypetes sp. No. 18	-	-	3	-	5	8
Protorhus deflexa	-	-	7	4	4	15

TABLE 7: Cont.

Sp.	Fruit	No Leaves	Adult leaves	Young leaves	Flowered	Total
South						
Mimosa sp. No. 033	21	2	-	19	-	42
Commiphora simplicifolia	14	6	5	8	-	33
Terminalia sp. No. 048	8	3	-	3	-	14
Grewia sp. No. 059	16	-	-	4	8	28
Alluaudia ascendens	-	1	3	2	2	8
Alluaudia procera	-	2	4	3	4	13
Commiphora Humbertii	3	-	12	14	-	29
Neobegnea mahafalensis	10	2	6	2	-	20
Diospyros Humbertiana	15	8	9	22	-	54
Commiphora orbicularis	5	4	5	3	-	17

TABLE 8: Number of sampled individuals differing with respect to each phenological category, irrespective of species, in each study area. (N=100. Number of species=10)

Northern Study Area

Month	Adult Leaves	Young Leaves	No Leaves	Flowers	Fruit
Jul.'70	12	8	12	0	20
Jul.'71	13	0	13	0	22
Aug.	20	0	12	0	21
Oct.	43	20	8	17	14
Nov.	36	31	4	13	7
Dec.	9	19	0	8	10
TOTAL	133	78	49	38	94

Southern Study Area

Jan.	4	27	2	6	33
Feb.	4	11	1	4	30
Mar.	0	10	0	0	14
Apr.	3	6	0	0	17
May	27	11	0	0	23
Sept.	29	37	32	14	16
TOTAL	67	102	35	24	133

rarer species, or could be a reflection of a gradual change in vegetation.

In both forests, most species occurred rarely in the sample circles and only a few species occurred in most or all of them. In Table 6, species are grouped according to the number of sample circles in which they occurred (results are also shown graphically in Figure 8). Thus, for example, in the north 62% of species occurred in only 10% of the sample circles (although not necessarily the same 10% - these figures refer only to frequency of occurrence and not to distribution). A Chi-Square test performed on the counts from each forest showed no significant difference between them.

There was, predictably, a close correlation between the number of sample circles in which a species occurred and the total number of individuals of that species counted.

Thus, concerning the distribution of tree species, it can only be said that a few species were abundant and widely, though not necessarily uniformly, distributed through the forest in each study area. Most species occurred rarely, unevenly scattered amongst the few dominant species.

Synchrony in fruiting/flowering etc.

The phenology of ten species was described each month in both study areas (see Figures 9 and 10). Ten individuals were sampled from each species. Comparison of the results indicates the degree of synchrony

1) among species within each forest (see Figure 11)

2) among individuals of each species (see Table 7 and Figures 9 and 10).

The "asynchrony counts" in Table 8 were estimated for each species for the whole period of the analysis by summing the total number of individuals with differing phenology each month. These individuals might differ with respect to any of the five phenological categories, i.e., no leaves, young leaves, adult leaves, fruit, flowers. The lower number of differing individuals was taken in each count: if two trees were fruiting and eight were not, the

asynchrony count was two. The higher the count the greater was the asynchrony.

This method had many shortcomings. 1) The biological interdependence of the different categories did not allow statistical comparison of the asynchrony counts. 2) In some cases, such as the two Alluaudia species, flowers were noted, but no fruit were seen. It is probable that at least some individuals that had flowered did subsequently produce fruit, so that my failure to see them artificially lowered the asynchrony count. 3) It made no distinction between synchrony of production and synchrony of carrying or availability. In Mimosa sp., No. 033, for example, drying seed pods had fallen from most trees by the middle of the dry season, but were found in a few trees right through the dry season. Yet the initial production of fruit in this species appeared to be well synchronized. However, in so far as this analysis aimed at assessing fluctuations in availability of food resources, the distinction between availability and production was unimportant. 4) More pertinent to the problem of relating gross fluctuations in phenology among species in each forest to abundance of food available to the animals was the impossibility of assessing the attractiveness of food to the animals. For example, fruit were found on Terminalia sp., No. 048, from January until April. By March, however, the fruit had begun to dry out on the trees and was no longer eaten in large quantities as in January and February. Thus its availability as a food source denoted in Figure 10 was more apparent than real. 5) Records noted only whether fruit, leaves, etc. were present or absent and gave no estimate of quantity.

For these reasons, the results presented below should be considered only as a crude tool for comparing and indicating possible trends in the periodicity of the forest in each study area.

Synchrony within species. The degree of synchrony between individuals of a food species may be important in determining both the period over which

animals included that species in their diet and what proportion of the diet it constituted when included. For example, the fruit of a closely synchronized species might be available in large quantities for a short period and constitute, temporarily, a major dietary item; the fruit of a loosely synchronized species, in contrast, might be available in small quantities over a long period and consistently make up a small proportion of the animals' diet.

In the south, species differed considerably in the synchrony of productio carrying of leaves, fruit, etc. Asynchrony counts ranged from 8-54. (The maximum difference in all phenological categories every month between individuals of a species would produce a count of 150.)

The closest synchrony was seen in each of the two Alluaudia species, which flowered and produced new leaves in September, and for the rest of the year bore adult leaves. The greatest degree of asynchrony was found in Diospyros humbertiana: although 5 individuals were without leaves in September, the other 5 had young leaves, and leaf production continued intermittently in individuals from January right through to June, although even by February there was still one individual without leaves. The production o fruit occurred in January, February and March, but by May all trees had lost their fruit. Mimosa sp., No. 033, showed a similarly persistent production of new leaves from September through till May. In this species the asynchrony count for fruit was high too, although this was probably a result of extended carrying by a few individuals (see above). All other species fell between these extremes of synchrony and asynchrony (see Table 7).

In the north, almost as much variation between species was found, with counts ranging from 8-46. Least variation was seen in Drypetes sp., No. 18, where new leaf production was seen in October only, and adult leaves were present during the rest of the study period. As in the Alluaudia species, this count may be artificially low in that, although flowers were observed,

no fruit was seen. Most variation was seen amongst individuals of Grevia sp., No. 121: in more than one month, individuals were found leafless but bearing fruit, while others were covered with young leaves.

Synchrony between species. The degree of synchrony between species in each forest may give a gross estimate of relative fluctuations in the frequency of the various phenological categories, irrespective of species. From this, tentative inferences can be made concerning fluctuations in the availability of different types of food.

There were similar trends towards interspecific synchrony in phenology in both study areas (see Figure 11 and Table 8). In both areas, a peak in leaf production coincided with a decrease in the presence of adult leaves. In the north this occurred at the onset of the wet season in October; in the south it occurred after light rainfall in September 1970, although the real wet season did not begin until January. In the north, flower production was at its height in October, and as the frequency of occurrence of flowers declined in December, the number of fruiting trees began to increase. In the south, fruit production reached a peak towards the end of the rains in February and March. The number of trees without leaves was at its height in north and south at the end of the dry season.

The south was an area of extreme seasonality with long periods of drought. The north had a more moderate climate. It is thus surprising that interspecific synchrony in the south was not consistently greater than in the north, given the harsh constraints of the southern climate. Looking at the allocation of scores between the different phenological categories in each area (Table 8), it is possible that the greater asynchrony count recorded for fruit in the south was the result of inaccurate data collection. The generally larger size and denser foliage of trees in the north made small fruit much more difficult to see. Failure to record the

presence of fruit would tend to lower the asynchrony count if 50% or less of the trees of a given species were carrying fruit. If more than 50% were carrying fruit, failure to note some of them would tend to increase the asynchrony count. Since the analysis in the northern study area was made during the first three months of the wet season when most species were flowering and producing young leaves, and during the latter part of the dry season, it is probably that less than 50% of trees were fruit-bearing at these times. If this is true, failure to count fruiting trees would indeed depress the asynchrony count.

The discrepancy in the "Young Leaves" counts tallies with descriptive notes made. Many trees in the north lost their leaves at the beginning of the dry season, although evergreen species retained their full foliage. By contrast, although the aridity in the south was much greater, some trees of many species continued to produce new leaves throughout the study period. This pattern differed from that of true evergreens, in that not all individuals of these species produced dry season foliage, and none of them maintained it throughout the dry season. It is possible that the evolution of water-conserving adaptations by many species in the south enables them to continue to produce new leaves well after the end of the short, or non-existent wet season, instead of resting dormant for nine months of the year. Such adaptations would not have evolved in the north, where rainfall is heavier and more evenly spread throughout the year.

SUMMARY

1) A description and analysis of the structure and composition of the forest in each study area was undertaken in order to provide detailed information on vegetation that might be useful in understanding seasonal and spatial variation in the ranging behaviour of P. verreauxi groups studied.

2) A total of 2,619 trees were described in the northern study area, and

3,136 in the south. The limited availability of time restricted the sample size. A count was made of the number of trees bearing lianas in order to provide a rough estimate of the frequency of lianas.

3) Two samples were made in each hectare square delineated by the grid system, and within each square these samples were randomly located. This followed the "stratified random" sample technique, and ensured that the total sample was well distributed over the total area to be sampled.

4) Each sample consisted of a circle with a measured radius of 5m. Within each circle, all trees with a trunk diameter greater than 3cm. at chest level were counted.

5) Tree height, maximum spread, and the height of the lowest branch above the ground were estimated by eye. Subsequent measurement of 200 trees showed that estimates were accurate to within ±2m.

6) Data on synchrony of leaf and fruit production and/or presence in tree species were based on observations made on ten species in each study area. Each month, observations on ten individual trees from each species were tabulated. Their phenology was classified into five categories: adult leaves, young leaves, flowers, fruit, dormant buds.

7) Mean density of trees in the two study areas was closely comparable: 109 per circle sampled in the north, and 105 in the south.

8) Other important differences did exist in the structure of the vegetation between the two areas. These concerned the ground layer, the abundance of foliage, and variation in the density of trees. In the south, the forest floor was relatively clear, where in the north it was often covered by dense woody and herbaceous shrubs. Both the abundance and the size of leaves was much greater in the north than in the south. The range of variation in density between sample circles was greater in the south than in the north. This was partly due to the inclusion of areas of exposed rock in samples in the south.

9) Trees in the north tended both to be taller and to have a greater maximum spread than in the south.

10) Many more species belonging to many more families were found in the north than in the south: at least 167 species, belonging to at least 35 families were collected in the north. In the south, the equivalent figures were only 70 and 23. These figures probably underestimate the actual diversity of species, since new species continued to be found throughout the analysis. Samples taken over a wider area would have revealed greater diversity, as a function of a progressive change in the composition of the vegetation.

11) In both forests, most species occurred rarely in the sample circles and only a few species occurred in most or all of them.

12) Asynchrony counts were estimated in order to compare degrees of synchrony among species within each forest and among individuals of each species.

13) In both study areas, individual species differed considerably in the synchrony of production/carrying of leaves, fruit, etc.

14) Synchrony between the various phenological categories in each study area as a whole, irrespective of species, was assessed. Similar seasonal trends were found in both study areas, and overall synchrony differed little. This was surprising in view of the extreme seasonality of the southern climate. It is suggested that tree species in the south may have evolved water-conserving adaptations enabling them to continue to produce new leaves in the dry season, and that this results in an asynchrony count comparable to that in the north.

SECTION III: HOME-RANGE SIZE AND UTILIZATION

INTRODUCTION

Throughout the field study, the ranging and feeding patterns of P. verreauxi were recorded using the techniques described in Part I. Three closely related aspects of the results, namely home-range size and utilisation, daily ranging patterns within that home-range, and dietary composition, are described in Sections IV, V and this Section. The discussion is reserved to the end of Section V, where an attempt is made to integrate these factors and to suggest the significance of the results of the vegetational analysis for them.

In keeping with the general theme of the study, particular attention was paid to seasonal and regional variation in patterns. The emphasis here is upon the distribution of activities through space: seasonality is the only aspect of the discussion that relates to the distribution of activities through time. When considering daily activity patterns (Section VI), the focus will be instead upon the relationship of certain activities to certain times of day.

Altmann and Altmann (1970), working with baboons, emphasized the influence of the distribution of vital resources such as water on home-range size and utilization, and Aldrich-Blake (1970) has discussed this question with reference to Cercopithecus mitis. It is to be assumed that in P. verreauxi also, and indeed in all forest-dwelling primates, there exists a relationship between the pattern of use of an area and the distribution of resources within that area. It is the aim of this section to investigate patterns of home-range use in P. verreauxi.

RESULTS

Problems concerning the definition and mapping of a home-range

The area over which all four study groups ranged was divided into 50m. squares, as described in Section II. If any member of a given group was seen in any one of those squares more than once, that square was said to constitute part of the home-range of that group. Jewell (1966) restated Burt's (1943) definition of "home-range" as follows: "...home-range is the area over which an animal normally travels in pursuit of its routine activities...." This definition is an approximate description of the home-ranges whose sizes are quoted below. It does, however, beg the important question of what constitutes an area over which an animal "normally travels." The criterion of occupancy on at least two occasions was introduced in this study to avoid including as "home-range" areas through which males, detached from their groups, occasionally moved. Much of the area covered by ranging males, particularly during the mating season, was never used by the rest of the group. Since this study was primarily concerned with the habitual movements of whole groups, a definition of home-range which excluded this component was necessary. It remains true, however, that the decision to include or exclude some areas was based on a fundamentally arbitrary criterion of "normality."

In addition to this problem of definition, there was a more practical one of accurate mapping. In this study, as stated, an animal had only to be in a square twice for the whole of that square to be included in the "home-range." This could have led to a gross overestimate of the real area occupied by the group. Unfortunately, in both study areas the flat ground provided no reference points, and the mapping of group movements on a scale finer than the 50m. grid was highly inaccurate during the first three months

TABLE 9: Home-range size, and area in which each group studied spent 95% of its time. The home-range size of five groups at Berenty is also shown (Jolly 1966)

Locality	Group	Group Size	Home-range size	Area in which group spent 95% of time
Northern study area	I	7	9.25 ha.	7.25 ha.
	II	4	9.25 ha.	8.50 ha.
Southern study area	III	6	8.75 ha.	6.75 ha.
	IV	4	8.75 ha.	7.00 ha.
Berenty	1		2.60 ha.	-
	2		2.60 ha.	-
	3		2.20 ha.	-
	4		2.20 ha.	-
	5		1.00 ha.	-

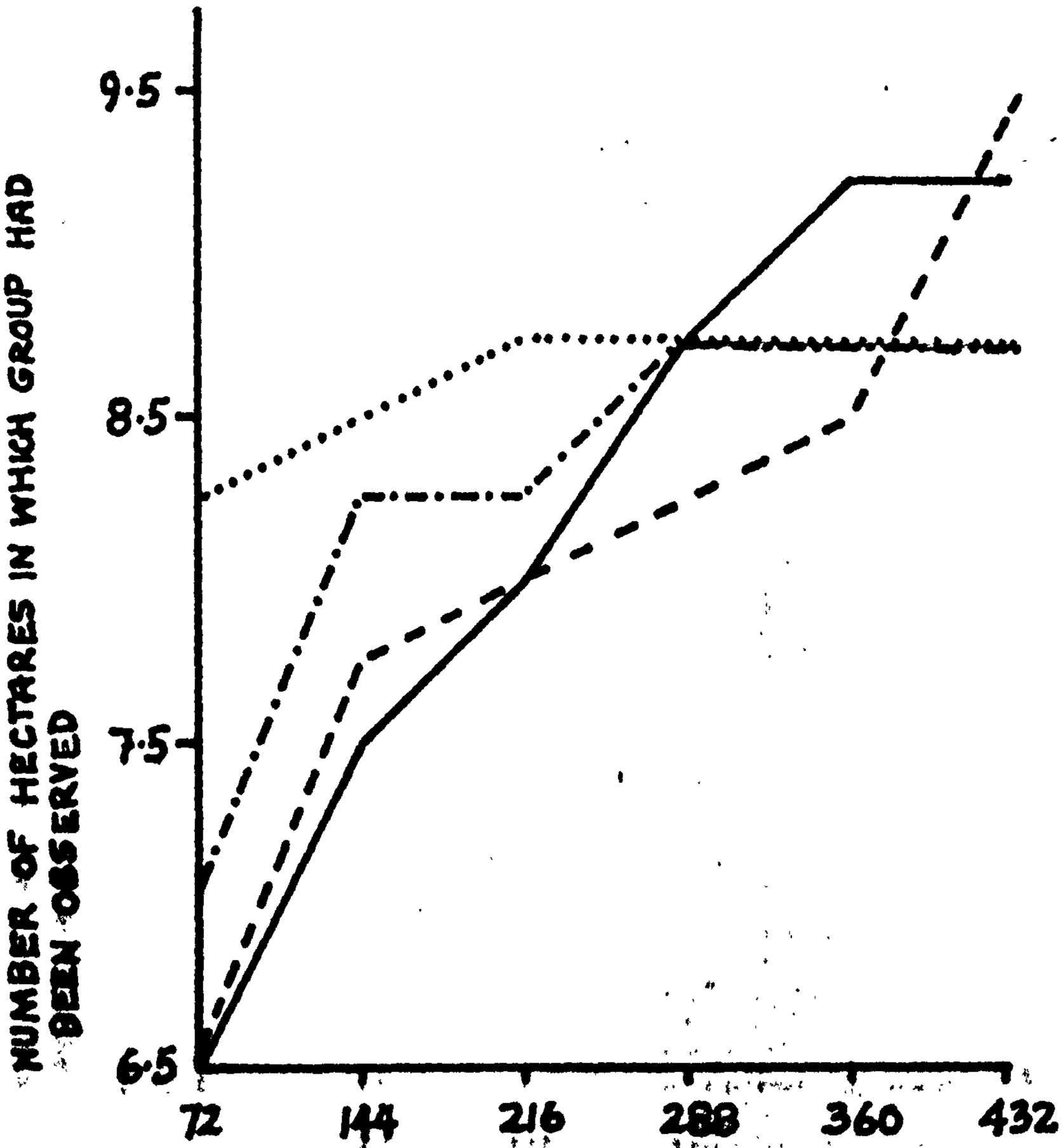
in each area. Later work when I was familiar with the study areas indicated that small, well-defined areas were present in the home-range of each group in which no animals were ever seen. It is thus regrettable that no finer techniques of mapping the movements of groups were used, and that the estimates of total home-range size given below are likely to be artificially inflated by the inclusion of small, unused lacunae within each square of the grid.

One further difficulty in estimating home-range size is the assessment of the use made of vertical space as opposed to horizontal space. Although time spent at specific heights in the forest has been referred to in various studies of primate species (Gartlan and Struhsaker, 1972; Jolly, 1966; Sussman, in press; Chalmers, 1968; Aldrich-Blake, 1970), these measures were ignored and only two dimensions considered in estimates of home-range size. Yet Sussman (in press) has shown important differences in the use made of the vertical component of a forest by Lemur fulvus rufus and Lemur catta. Studies of feeding behaviour in birds have also shown use of the vertical component of a habitat to be an important variable (Hartley, 1953; Stallcup, 1968). In this study, the distribution of trees between height categories did not differ significantly between north and south (see Section II), and animals distributed their time quite evenly between the different height categories in both study areas (see Section VI). Thus comparisons of home-range size using horizontal measures only are probably valid. Such comparisons could be misleading, however, between areas with very different vertical components or between species making different use of the vertical component.

Home-range size

Table 9 lists the estimated home-range size for the groups studied, according to the definition of home-range given on P. 124. The area in

Fig. 12. Increase in total area over which groups had been observed to range, as a function of increased time spent watching each group.

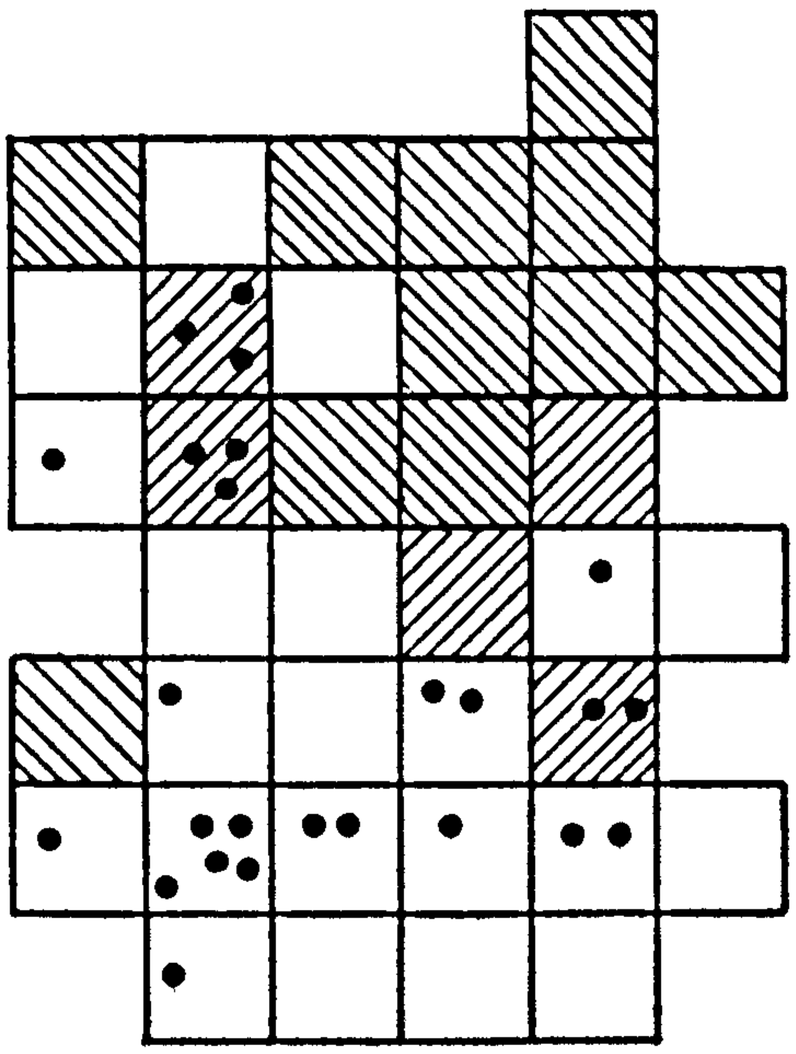

GROUP I
GROUP II
GROUP III
GROUP IV
9·5
8·5
7·5
6·5
72
144
216
288
360
432
NUMBER OF HECTARES IN WHICH GROUP HAD BEEN OBSERVED
NUMBER OF HOURS SPENT WATCHING EACH GROUP

which each group spent 95% of its time is also given in Table 9. This shows that all four groups used a relatively large proportion of their "home-range" very rarely. For example, Group I spent only 5% of its time in approximately one-fifth of its "home-range." Definitions apart, it is a moot point whether Group I really "normally travelled" through such parts of its home-range, and the figures are included to illustrate the essential arbitrariness of estimates of home-range size, referred to on P. 124. However, between the four groups there was no significant difference in either estimated home-range size or the area in which each spent 95% of its time.

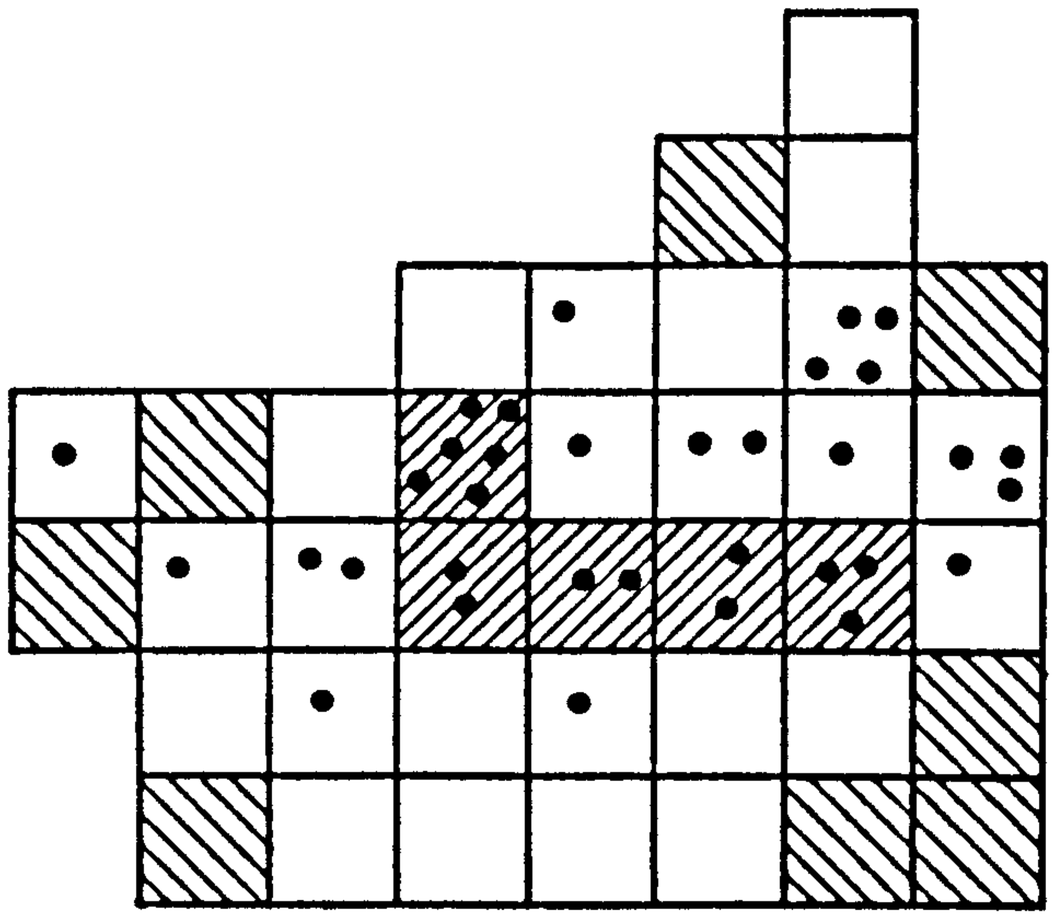
Figure 12 shows that observed home-range size increased with time spent watching each group. The rate of apparent home-range size increase was initially more rapid for Groups III and IV then for Groups I and II. Thus the increase was not simply related to the number of hours over which each group had been observed, but to the season in which observations were made: the total number of squares entered and the number of different squares entered per unit time increased in the wet season in all four groups (see Section IV). The initially greater rate of increase in the south was due to records being started in the wet season, whereas records for the northern groups were begun in the dry season. If the data are re-ordered so that the southern groups' records begin in the dry season, and the northern groups' in the wet season, the reverse situation is found, i.e., for the first three months, the home-range estimates for Groups I and II exceed those for Groups III and IV. This observation of the modifying effect of seasonal differences on the rate of apparent increase in home-range size indicates that the rate of increase cannot be assumed to be comparable within, and certainly not between, species. Comparisons of home-range size should thus be made only when the curve plotting the rate of apparent increase in home-range size reaches an asymptote.

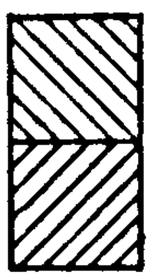
Fig. 13. Areas of exclusive use, foci of activity, and the locations of inter-group interactions within the home-range of each study group.

GROUP I



GROUP II



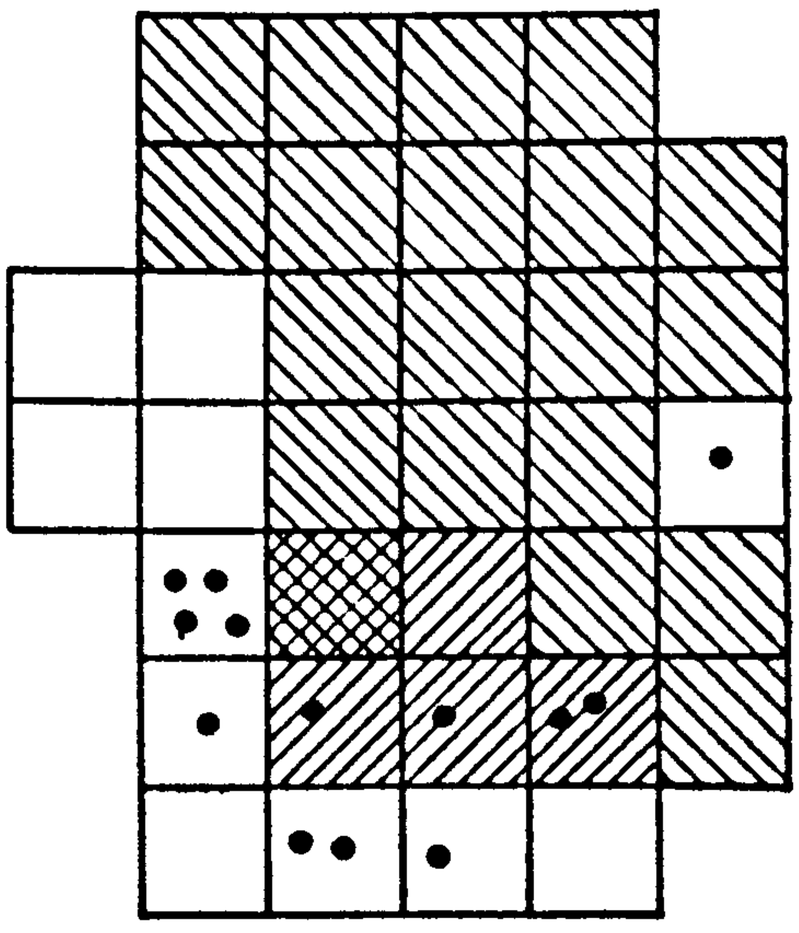


Area of exclusive use

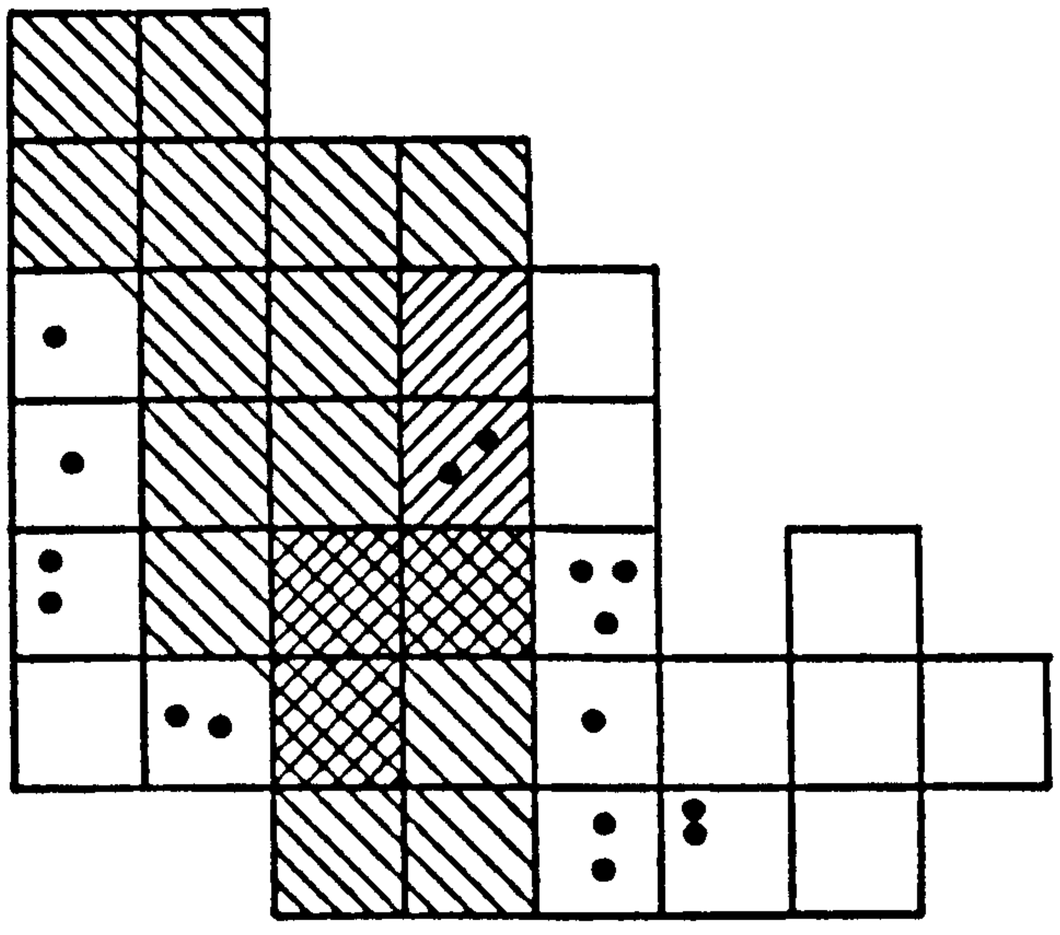
Foci of activity

Intergroup interactions

GROUP III



GROUP IV



The estimated home-range size of five groups at Berenty (Jolly, 1966), given in Table 9, was almost one quarter that of groups in the present study. Although estimates of home-range size may be biased by the length of time over which observations were made, and the season in which a time-block of observations was carried out, there was probably a real difference between home-range size at Berenty as opposed to the northern and southern study areas where results were closely comparable. Jolly (1966) estimated home-range size of the Berenty groups after 255 hours of observation (a maximum of 51 hours per group). In the present study, after 72 hours of observation per group, apparent home-range size of all four study groups was already between two and three times the size of those recorded by Jolly (see Figure 12).

Differential utilization of home-range

The four study groups all used some parts of their home-range much more heavily than others. Group I spent between 20 and 60% of their time each month in the same five squares of their home-range. These were the first five when squares were ranked according to frequency of use and total time spent in them. If Group I's time had been evenly distributed throughout their home-range, they would have been expected to spend only 13.5% of it in any five squares; Group II spent between 25 and 40% of their time in five squares instead of an expected 13.5%. In the south, Groups III and IV spent between 50 and 75% of their time each month in five squares instead of an expected 14.9%.

Kaufmann (1962) used the term "core area" to describe "...a particular part of the home-range...used more frequently and with greater regularity than other parts..." Carpenter's term "foci of activity" seems more appropriate than Kaufmann's "core area," however, to describe the heavily used squares in the study groups' home-ranges. Figure 13 shows that these

Fig. 14. Time spent each month in the five squares most used overall by Group II.

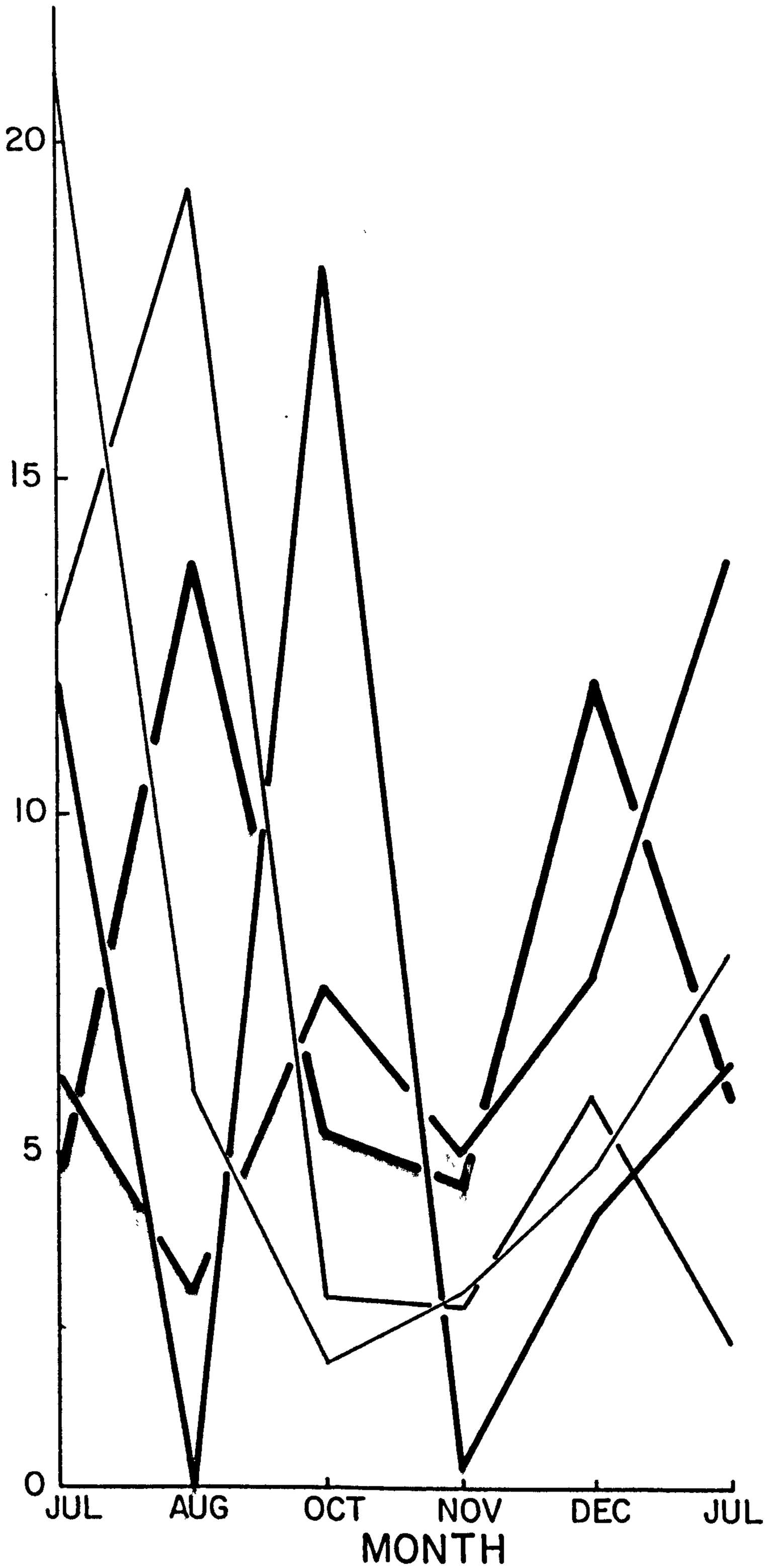
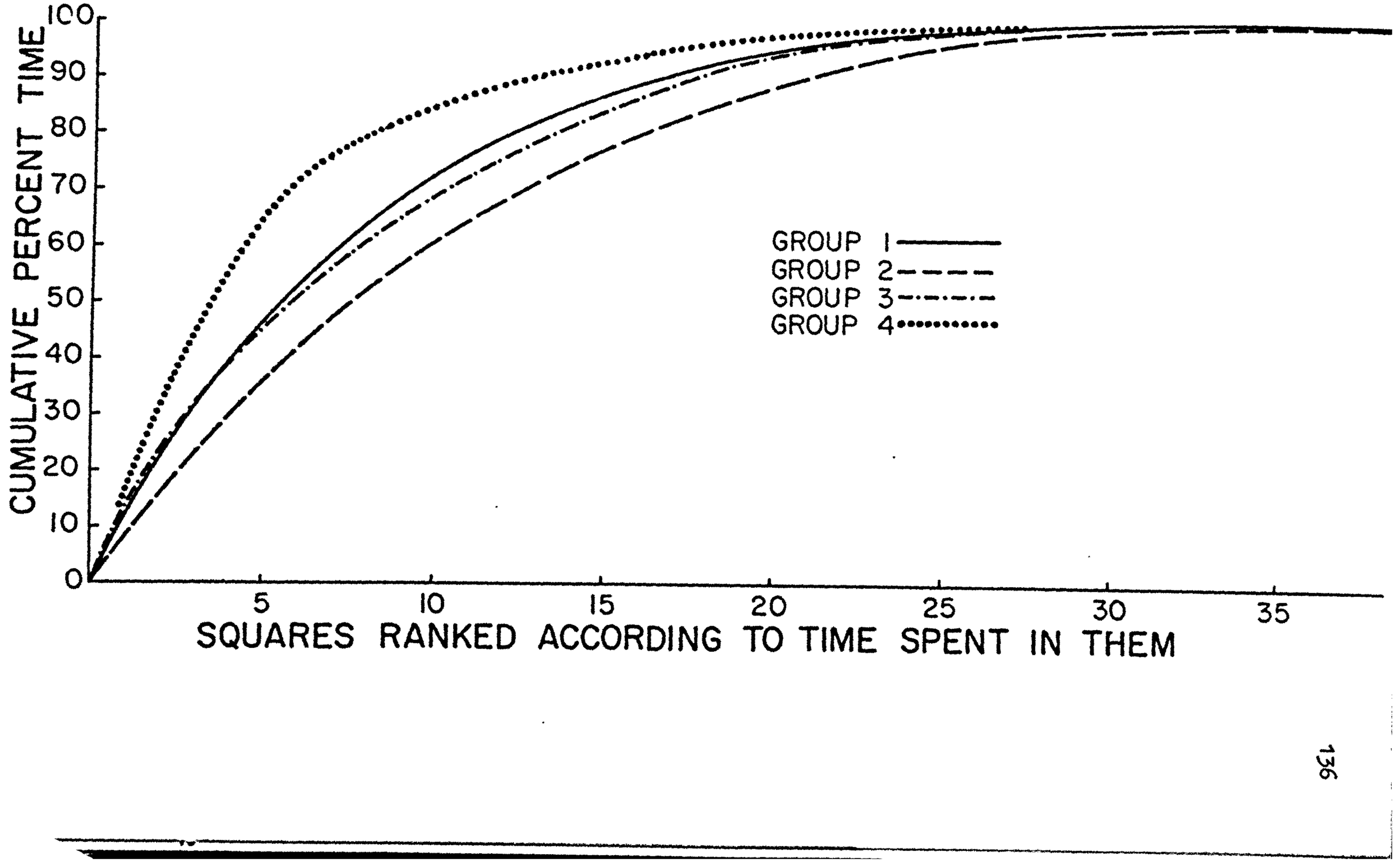

20
15
10
5
0
PERCENT TIME
JUL
AUG
OCT
NOV
DEC
JUL
MONTH

Fig. 15. Variation between each group's allocation of time across its home-range.


CUMULATIVE PERCENT TIME
100
90
80
70
60
50
40
30
20
10
0
5
10
15
20
25
30
35
SQUARES RANKED ACCORDING TO TIME SPENT IN THEM
GROUP 1
GROUP 2
GROUP 3
GROUP 4

squares were not necessarily grouped together within each group's home-range, so that they cannot be described as a composite, "...particular part of the home-range..." Although each group used these squares overall "...more frequently and with greater regularity than other parts...", there was considerable variation in time spent in them from month to month. Figure 14, using data from Group II, shows that when each square is considered alone, there were some months when it might not be occupied at all. This is also true for the other three groups. In addition to removing criteria of spatial integrity, use of the term "foci of activity" reduces Kaufmann's emphasis on regularity of use.

As with definitions of home-range, it should be noted here that the choice of areas to be designated "foci of activity" was inevitably an arbitrary one, and the classification artificial rather than real.

While all four groups tended to use a relatively small area of their home-range more intensively than the rest of it, throughout the study, there were considerable differences in the extent to which each group showed this tendency. Figure 15 shows the variation between groups' allocation of time across their home-range. Squares were ranked according to the amount of time spent in them, and the time spent in them is shown cumulatively as a percentage of total time. The inter-dependence of observations prevented statistical analysis of the significance of the differences found. However, it is clear that there was no consistent variation between regions. The causes of this differential utilization of the home-range should thus be sought at the level of variations in individual ranges rather than at the level of major ecological variations between regions. The uneven distribution of tree species in the forests in both study areas was referred to in Section II. From this it can be inferred that important variations in the size, abundance and distribution of food sources probably

Fig. 16. Seasonal differences in the distribution of time between squares by the groups in each study area.

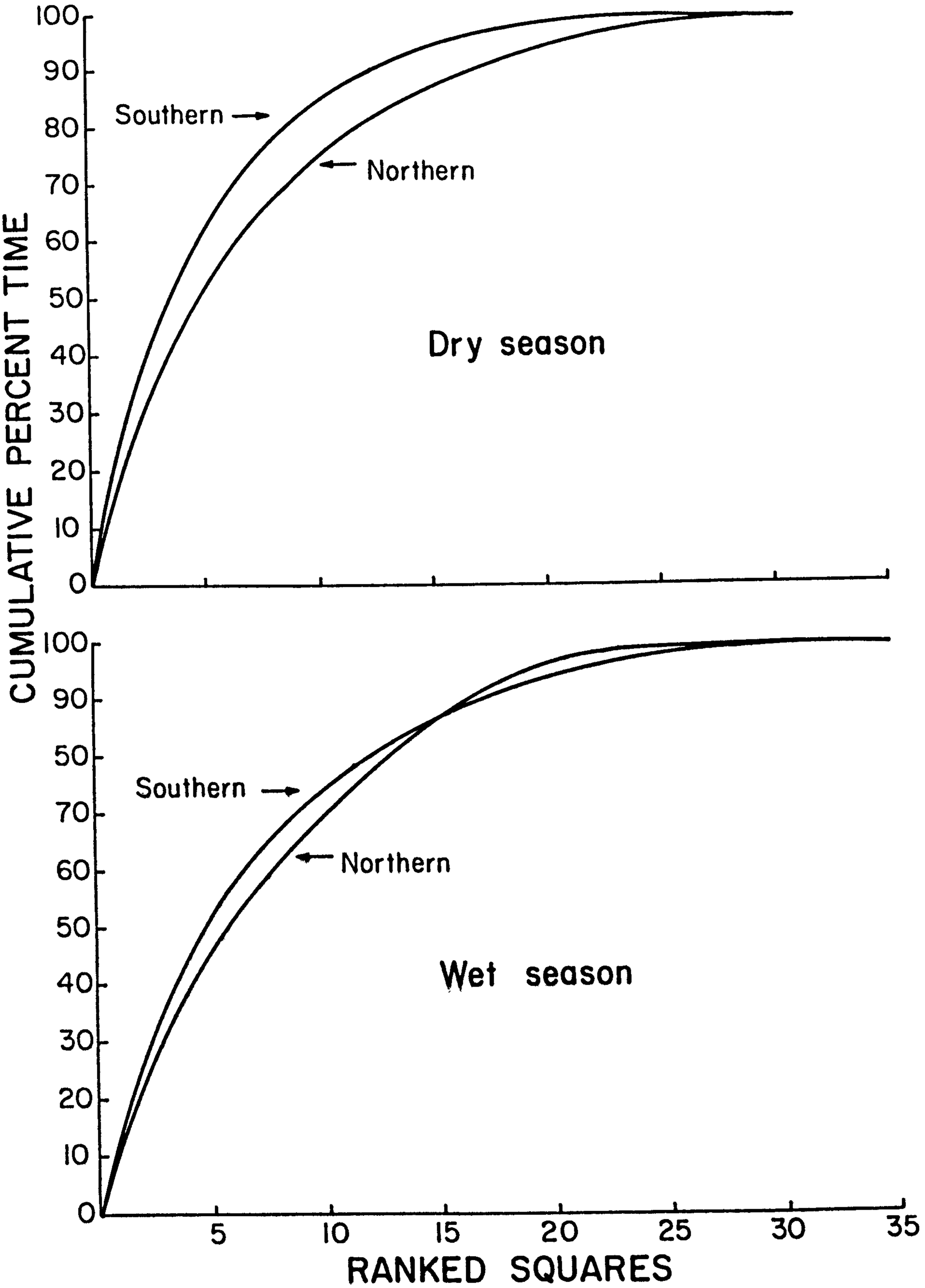

CUMULATIVE PERCENT TIME
100
90
80
70
60
50
40
30
20
10
0
Southern
Northern
Dry season
100
90
50
70
60
50
40
30
20
10
0
Southern
Northern
Wet season
5
10
15
20
25
30
35
RANKED SQUARES

TABLE 10: Monthly analysis of the nature of activity taking place in the foci of activity for each group

Group	Month	Time in foci of activity: Feeding	Non-feeding
I	July	53.3%	49.9%
	Aug.	19.7%	22.3%
	Oct.	38.3%	29.5%
	Nov.	42.0%	31.0%
	Dec.	53.2%	72.6%
	July	57.2%	56.0%
Overall mean		43.2%	
II	July	38.4%	38.7%
	Aug.	48.0%	37.3%
	Oct.	33.8%	20.5%
	Nov.	38.2%	35.0%
	Dec.	36.1%	26.1%
	July	24.9%	33.2%
Overall mean		34.3%	
III	Jan.	31.2%	31.1%
	Feb.	58.1%	75.8%
	Mar.	41.0%	37.3%
	Apr.	48.0%	53.3%
	May	29.5%	46.7%
	June	40.5	79.8%
	Sept.	50.8%	57.3%
Overall mean		48.3%	
IV	Jan.	39.4%	63.3%
	Feb.	43.3%	58.8%
	Mar.	61.2%	87.5%
	Apr.	54.0%	73.3%
	May	41.3%	69.3%
	June	49.8%	69.2%
Overall mean		59.2%	

existed between home-ranges located within each general habitat type. It is likely that the variation between groups in patterns of home-range use was related to highly localized environmental variation of this kind.

Regional distinctions can be made when considering seasonal changes in home-range utilization. When data from the wet and dry season are considered separately (see Figure 16), seasonal differences become apparent in the distribution of time between squares by the groups in each study area. In both study areas, the groups showed a tendency to spend more time in fewer squares in the dry season. This tendency was much more pronounced in the south than in the north. Factors that may contribute to this regional difference are discussed in Section V.

Although parts of each home-range could be differentiated between according to time spent in them, no differentiation could be made according to the type of activity performed. In Table 10, an analysis is given of the main ways in which time was spent by each group in their foci of activity. The time spent feeding/not-feeding in the foci of activity is expressed as a percentage of total time spent feeding/not-feeding anywhere in the home-range each month. It is apparent that these foci were not simply sleeping sites or areas of particularly intensive feeding, but rather that all animals both fed and rested in them for a high proportion of time. This held good throughout the home-range. There was a highly significant correlation between the amount of time spent feeding and the amount of time spent in other activities in all squares for all four groups (Spearman Rank Correlation Coefficient r_s=0.85, N=37, p≤.01 - Group I; r_s=0.72, N=38, p≤.01 - Group II; r_s=0.80, N=35, p≤.01 - Group III; r_s=0.81, N=35, p≤.01 - Group IV). Although some correlation was inevitable, a very close correlation was not, since the animals only spent a small percentage of their time feeding and could have fed in some squares and used other squares exclusively for activities other than feeding.

TABLE 11: Number of squares used by other groups among the ten least, and the ten most, used squares of each study group.

Group	No. of squares in which overlap occured amongst the 10 least used squares in the home-range	No. of squares in which overlap occured amongst the 10 most used squares in the home-range
I	7	8
II	10	10
III	2	3
IV	4	4

Within each square there were preferred sleeping trees which were usually used when the group was in the square for the night. However, they did not resort to certain trees with the regularity and predictability of baboons (see Altmann and Altmann, 1970). Although sleeping trees were often large, on several occasions groups were found sleeping only 5m. from the ground on the branches of a small tree. In the south, there seemed to be a preference for Alluaudia ascendens, but insufficient data are available for a statistical analysis.

Exclusivity of use of home-range

One important aspect of ranging behaviour in P. verreauxi was the nature of inter-group relations. The four study groups each had zones within their home-ranges in which no other groups were seen. These are marked on Figure 13 and are referred to as "monopolized zones." A square was said to be part of a monopolized zone if no other group was found in it more than once, and to be part of an overlap area if another group was found in it more than once. As with estimates of home-range size, this method overestimated the real area of overlap, and results are undoubtedly inflated.

Exclusivity of use was not related to amount of use. Areas constituting foci of activity were not necessarily monopolized zones and, conversely, little used squares were not necessarily areas of overlap. An analysis of the most and least used squares in the home-range of each study group was made. It showed that an almost equal number of each group's most and least used squares were also entered by other groups (see Table 11).

In the north, Groups I and II had exclusive use of 29% and 24% of their total home-ranges. These areas of exclusive use were composed of widely scattered monopolized zones which were often located on the periphery of the home-range. It is possible that they were simply areas in which, by

chance, I did not see other groups or that some of them were areas which no groups visited often and that, consequently, no other groups were seen in them more than once. Inter-group interactions occurred all over the home-range of each group (see Figure 13), so it is improbable that the groups were defending the monopolized zones or the boundary of some other well-defined area during these encounters. Little hostility was apparent in many of the 59 encounters observed in the north: only 18 culminated in the ritualized "battle" described by Jolly (1966). Most of these "battles" occurred with reference to a particular food source in which one of the groups was feeding prior to the encounter. In most other instances, after reciprocal staring and some grunting the groups moved away from each other towards the geographical centre of their home-range (a full description of inter-group encounters is in preparation).

In the south, Groups III and IV had exclusive use of 54% and 51% of their home-range. Figure 13 shows that, in contrast to the scattered distribution of monopolized zones in the north, the exclusively used areas of each group in the south formed one block. Inter-group encounters occurred on the periphery of this block. It appeared that the groups had clear borders to their monopolized zones, defined by periodic hostile encounters with neighbouring groups. Only 29 encounters were observed in the south (outside the mating season), but all except 9 culminated in "battles."

The concept of territoriality has been variously defined and applied to many mammalian and bird species (see Noble's review, 1939). Burt (1943) accepted Noble's definition of territory as "any defended area," but Pitelka (1959) proposed that "...territory should be defined as an exclusive area, not merely a 'defended' one..." Jewell (1966) called this a "monopolized zone," distinct from "core area" or "foci of activity" in that the latter may be used by other groups too. He went on to point out that

the exact way in which such a zone is maintained by a group is not known. He cited the "monopolized zones" of groups of soay sheep as an example of areas used exclusively by one group and yet not, apparently, defended in any sense.

Taking Pitelka's definition of territoriality, all four groups had a territory. However, since most primates are territorial in the sense of having areas within the home-range of each group that are used exclusively by that group, it is more useful to consider territory as a defended area. Using this criterion, there seems little justification for calling the northern groups territorial: with scattered monopolized zones, and inter-group encounters taking place throughout the extensive overlap areas, it cannot be held that these encounters defined the geographical boundary of a defended area. In contrast, the evidence suggests that, in the south, each group did have a territory: the area of overlap between groups was narrow and hostile inter-group encounters occurred round the periphery of a single, central monopolized zone, or territory, in each home-range. The presence of apparently territorial behaviour in the south, and its absence in the north, may represent one of the few gross behavioural differences between groups in the two study areas.

SUMMARY

1) The aim of this section was to investigate patterns of home-range use in P. verreauxi.

2) The area over which all four study groups ranged was divided into 50m. squares. If any member of a given group was seen in any one of those squares more than once, that square was said to constitute part of the home-range of that group. This avoided the inclusion of areas covered by ranging males, particularly during the mating season, which were never used by the rest of the group.

3) An animal had only to be in a square twice for the whole of that square to be included in the "home-range." This probably led to a gross over-estimate of the real area occupied by the group, but more accurate mapping was impossible in the initial stages of the study, due to my lack of familiarity with the terrain.

4) Home-range, as defined in this study, did not include an assessment of the use made of the vertical component of the habitat. The distribution of trees between height categories did not differ significantly between north and south, and animals distributed their time quite evenly between the different height categories in both study areas. Thus comparisons of home-range size using horizontal measures only are probably valid. Such comparisons could be misleading, however, between areas with very different vertical components or between species making different use of the vertical component.

5) Home-range size varied between 9.25ha. and 8.75ha. However, all four groups used a relatively large proportion of their home-range very rarely. There was no significant difference in either estimated home-range size for the four groups or in the area in which each spent 95% of its time.

6) Observed home-range size increased with time spent watching each group. Seasonal differences were found to modify the rate of apparent increase in home-range size. This was because the total number of squares entered and the number of different squares entered per unit time was greater in the wet season than in the dry, for all four groups.

7) Estimated home-range size of five groups at Berenty was almost one quarter that of the groups in this study. Although estimates of home-range size may be biased by the length of time over which observations are made, and the season in which a time-block of observations is carried out, there was probably a real difference between home-range size at Berenty as opposed to the northern and southern study areas.

8) The four study groups all used some parts of their home-range much more heavily than others. These areas were not necessarily clumped together, and were called "foci of activity." There were considerable differences in the extent to which each group showed this tendency towards intensive use of a small area of the home-range, but the variation was not related to gross regional differences. The causes of this differential utilization of the home-range should thus be sought at the level of variations in individual ranges.

9) It was possible to make regional distinctions when considering seasonal changes in home-range utilization. In both study areas, the groups showed a tendency to spend more time in fewer squares in the dry season, but this tendency was much more pronounced in the south than in the north.

10) No differentiation could be made between parts of the home-range according to the type of activity performed in them. In the foci of activity, for example, animals both fed and rested for a high proportion of time.

11) The four groups each had zones within their home-ranges in which no other groups were seen. These were called "monopolized zones." Exclusivity of use was not, however, related to amount of use. In the north, areas of exclusive use were composed of widely scattered monopolized zones which were often located on the periphery of the home-range. Inter-group encounters occurred all over the home-range of each group, so it is improbable that the groups were defending the monopolized zones or the boundary of some other well-defined area during these encounters. Little hostility was apparent in many of the encounters observed. In the south, the groups studied had exclusive use of a larger area of their home-range than in the north. The exclusively used areas of each group formed one block, and inter-group encounters occurred on the periphery of this block.

It appeared that the groups had clear borders to their monopolized zones, defined by periodic hostile encounters with neighbouring groups.

12) Taking "any defended area" as a definition of territory, there seems little justification for calling the northern groups territorial. In contrast, the evidence suggests that, in the south, each group did have a territory. The presence of apparently territorial behaviour in the south, and its absence in the north, may represent one of the few gross behavioural differences between groups in the two study areas.

SECTION IV: RANGING BEHAVIOUR

INTRODUCTION

The spatial displacement of the animal under observation each day was recorded at minute intervals (see P. 37). Distances were estimated by eye and are therefore approximate. A rough check on accuracy could be kept, however, because it was known that an animal had to move at least 50m. in order to cross two parallel trails of the grid system.

Differential utilization of the home-range over large units of time was discussed in Section III. Here, the analysis is of daily ranging behaviour, of seasonal changes in daily patterns, and of the relationship between movements each day and overall home-range utilization.

RESULTS

Regularity of ranging

All four groups visited most parts of their home-range within ten to twenty days, but although general patterns of movement recurred, there was no evidence of a regular, predictable cycle during which all parts of the home-range were visited. Clutton-Brock (in press) found regularities in the rate of movement of a group of Colobus badius around its home-range: the group visited most parts of the home-range in a predictable number of days. Since only six days of data were collected per group per month in this study, it was not possible to demonstrate, if indeed it existed, the presence of comparable regularities in P. verreauxi. Subjective impressions suggested that groups in both study areas visited most parts of their home-range within ten to twenty days. However, although some kind of sequential use of different parts of the home-range occurred, there seemed to be considerable variation from month to month, even within the same

Fig. 17. Mean distance moved each day, each month, for each group.

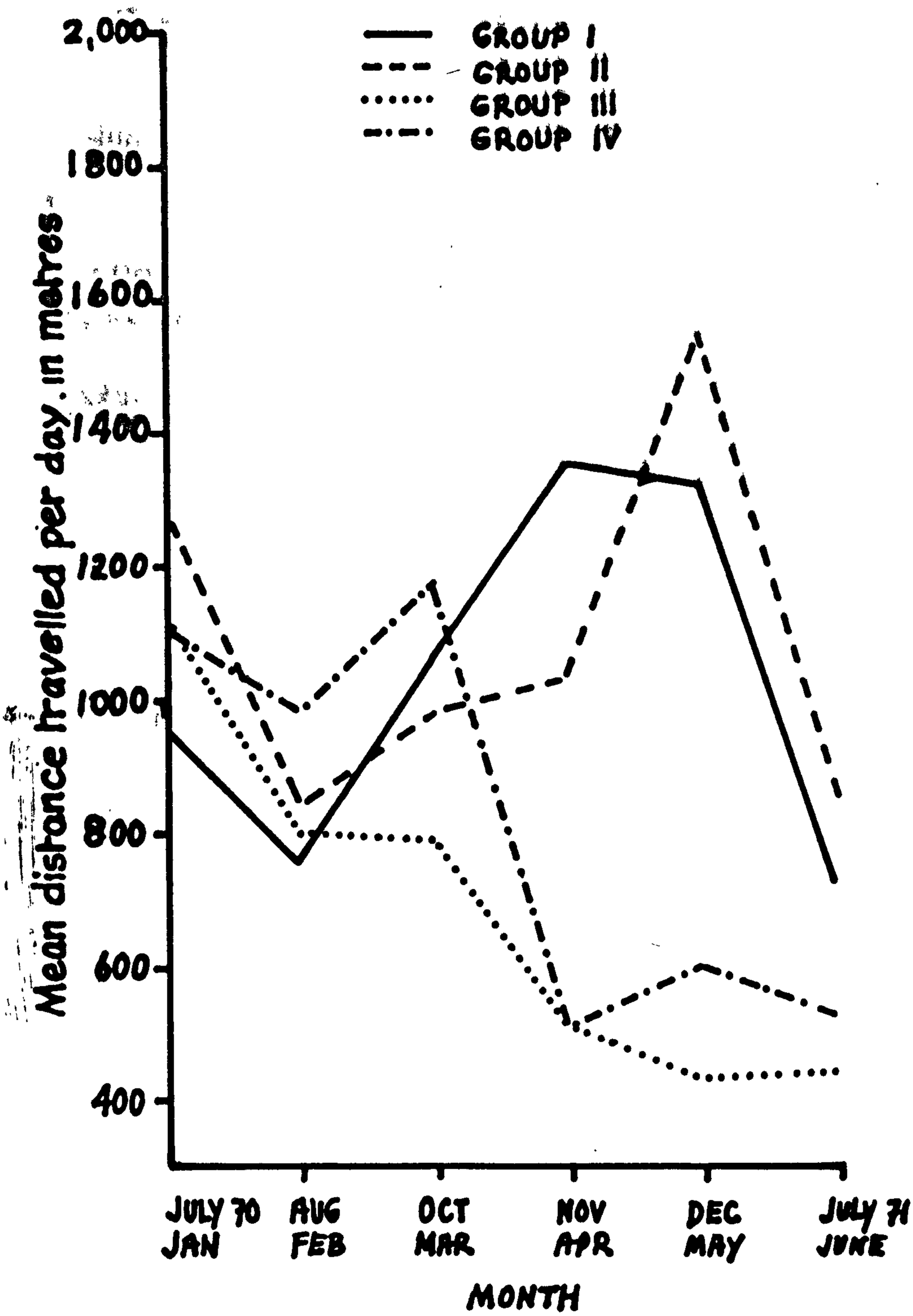

GROUP I
GROUP II
GROUP III
GROUP IV
Mean distance travelled per day. in metres
2,000
1800
1600
1400
1200
1000
800
600
400
JULY 70 JAN
AUG FEB
OCT MAR
NOV APR
DEC MAY
JULY 71 JUNE
MONTH

TABLE 12: Range of variation in daily distance moved by each group

Group	Month	Mean distance moved*	Range of Variation*
I	July	959	677-1294
	Aug.	760	706-1003
	Oct.	1064	818-1252
	Nov.	1352	1120-1530
	Dec.	1322	1201-1513
	July	727	533-944
II	July	1279	953-1842
	Aug.	845	694-1003
	Oct.	983	646-1224
	Nov.	1034	834-1641
	Dec.	1548	1329-1764
	July	852	690-956
III	Jan.	1124	1201-1513
	Feb.	807	404-1177
	Mar.	792	666-1035
	Apr.	513	457-671
	May	438	342-571
	June	447	435-524
IV	Jan.	1104	621-1906
	Feb.	985	643-1607
	Mar.	1177	662-1607
	Apr.	513	322-869
	May	608	434-775
	June	529	348-637

* Results are given in metres

season, in the time it took to cover the entire home-range. I think it unlikely that further research would reveal a well-defined cycle such as that found in C. badius at Gombe Stream.

No analysis was made of actual routes taken by the animals. In the early stages of the study it was difficult to re-identify pathways through the trees and, subsequently, the problem became one of definition: animals frequently moved along the same general line on successive days, but rarely through exactly the same sequence of trees, and for purposes of quantification it was impossible to find a criterion by which to decide whether a given animal was "on" the route or "off" it. Characteristically, each group followed the same general patterns and direction of movement for two or three days, usually feeding in the same trees each day, and then suddenly both the sleeping tree and the ranging pattern would change.

While on the one hand groups were seen to follow certain general routes intermittently throughout the field study, on the other hand day ranges frequently did not conform to any previously established pattern, or began along known routes and then veered off unpredictably.

Variation in distance moved each day

There was an overall difference in the mean daily distance moved between the groups, and within each group there was a significant difference between seasons. Figure 17 shows the mean distance moved each day, estimated from the distance moved by six individuals on six separate days, each month, for each group. The range of variation in daily distance moved is shown in Table 12.

Recordings were made on individual animals (P. 38), but the results may be considered to represent the ranging behaviour of the group as well as of the subject under observation: a Kruskal-Wallis One-way Analysis of Variance showed no significant difference in the distance moved by the

TABLE 13: Number of squares entered, number of different squares entered, and the ratio between them, for each group for each month.

Group	Month	No. squares entered	No. different squares entered	Ratio
I	July	69	22	3.1
	Aug.	62	20	3.1
	Oct.	118	23	5.1
	Nov.	144	25	5.8
	Dec.	137	26	5.3
	July	69	17	4.0
II	July	90	24	3.7
	Aug.	79	21	3.8
	Oct.	122	23	5.3
	Nov.	121	26	4.6
	Dec.	167	27	6.2
	July	85	31	2.7
III	Jan.	119	27	4.4
	Feb.	88	23	3.8
	Mar.	95	19	4.0
	Apr.	69	20	3.4
	May	63	19	3.3
	June	55	17	3.2
IV	Jan.	137	25	5.5
	Feb.	107	24	4.4
	Mar.	130	20	6.5
	Apr.	69	21	3.3
	May	56	18	3.1
	June	64	17	3.8

* Ratio = $\frac{\text{Total No. of Squares}}{\text{No. of different squares}}$

different age/sex classes, so the data were considered together. Although the group usually moved as a cohesive unit, this result was not inevitable since all displacements, including minor "circular" movements, were recorded, and it was possible that differences in general levels of activity, or restlessness, could have existed between age/sex classes.

There was no significant difference between the distance moved by each group in each study area, so data from the two groups in each study area were combined. It was estimated that in the north, the mean distance moved each day in the wet season was 1,100m; in the dry season it was 750m. In the south, the mean distance moved each day in the wet season was 1,000m; in the dry season it was 550m. Thus throughout the study period, the northern groups ranged further, on the average, each day than the southern groups (Mann Whitney U Test, $N_1=N_2=12$, $U=34$, $p \leq .025$).

In both north and south, groups moved further each day in the wet season than in the dry season (Mann Whitney U Test, $N_1=N_2=6$, $U=0$, $p \leq .001$ - South; $N_1=N_2=6$, $U=3$, $p \leq .008$ - North). This decrease in the distance moved each day in the dry season is shown in Figure 17.

Relationship between distance moved and area covered

In all four groups, distance moved per day increased significantly during the wet season. At the same time, there was a slight increase in the number of different squares entered and a larger increase in the total number of squares entered during the six-day observation block. These results are shown in Table 13, together with the associated change in the ratio between these measures. They suggest that, in ranging further in the wet season, groups tended merely to cover the area, or home-range, used in the dry season more rapidly in the wet season, rather than to expand it appreciably.

SUMMARY

1) All four groups visited most parts of their home-range within ten to twenty days, but although general patterns of movement recurred, there was no evidence of a regular, predictable cycle during which all parts of the home-range were visited.

2) Animals frequently moved along the same general line on successive days, but rarely through exactly the same sequence of trees. Although certain general routes were followed intermittently throughout the field study, day ranges frequently did not conform to any previously established pattern, or began along known routes and then veered off unpredictably.

3) There was an overall difference in the mean daily distance moved between the groups in each area, and within each group there was a significant difference between seasons. There was no significant difference in the distance moved between the different age/sex classes, nor between the two groups in each study area. The northern groups ranged further, on average, each day than the southern groups, and all four groups ranged further each day in the wet season than in the dry.

4) There was a slight increase in the number of different squares entered and a larger increase in the total number of squares entered during each six-day observation block in the wet season. This suggests that, in ranging further in the wet season, groups tended merely to cover the area, or home-range, used in the dry season more rapidly in the wet season, rather than to expand it appreciably.

SECTION V: DIET AND FEEDING BEHAVIOUR

INTRODUCTION

This Section describes the general characteristics of feeding behaviour in the groups of P. verreauxi studied, seasonal and regional variations in the composition of their diet, and the distribution of food sources. In the final discussion, an attempt is made to integrate the results given in this Section with those in Sections III and IV.

The low stature of the forest in each study area, plus the extreme habituation of the study animals and, in the south, the low density of foliage, all facilitated accurate observation of the food species and part being eaten. The only problem has been the subsequent difficulty in some cases in identifying tree species.

An animal was said to be feeding when it was chewing the bark, buds, leaves, flowers or fruit of a plant species. An animal was said to be foraging when its nose or hand was in contact with a food source. There may be an important relationship between the time spent foraging for a given food species and the amount of time spent feeding on that species; in a study of the feeding behaviour of the Great Tit, Royama (1970) found a relationship between the amount of a given food that a predator collects and the amount of effort needed to hunt the prey species. He described this relationship in terms of "profitability," the most "profitable" food being that which gave the greatest energetic input for the least energy expenditure. Unfortunately, in this study the operational definition of foraging was such as to under-estimate the real time spent foraging, because it took no account of occasions when an animal sat looking round for food. The latter activity could not be included in the foraging category because no satisfactory, consistent criteria were found by which

to score it. With this knowledge of the probable inaccuracy of the data, no analysis of foraging behaviour was made. It is mentioned here merely to indicate that such a relationship may have been present, although no analysis of it was possible.

RESULTS

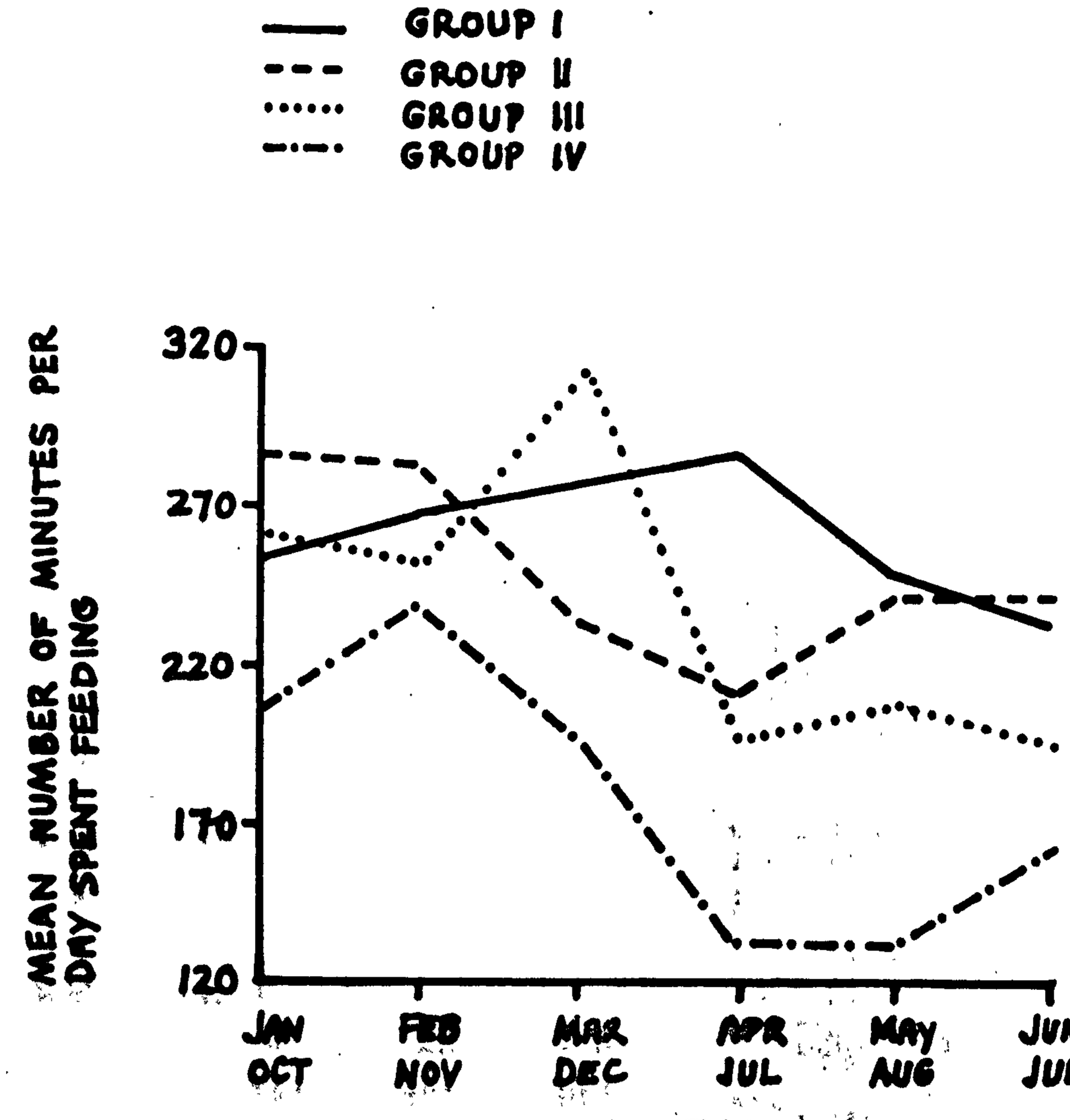
General characteristics of feeding behaviour

Timing of feeding bouts. In both study areas, there were certain periods of the day when feeding was the main on-going activity, although other activities did occur briefly at these times. These periods are called "feeding bouts." In the wet season, all groups tended to have two feeding bouts, one in the morning and one in the afternoon, lasting from one to three hours each. In the dry season, there was one main feeding bout which reached a peak towards midday (see Section VI).

Intensity of feeding bouts. The intensity of feeding, or the rate at which food was eaten, varied considerably within these bouts. At some point during most bouts, the entire group was to be found feeding in a single tree over a prolonged period lasting up to two hours. On 235 occasions in the north, and 85 in the south, four or more animals were observed feeding in the same tree. For the rest of the bouts, animals usually dispersed and moved quite rapidly from tree to tree, feeding briefly in each. These variations in the intensity of eating and in inter-animal distance during bouts were probably related to variations in the size and density of food sources as well as to varying degrees of tolerance of proximity between group members.

Feeding postures. Many feeding postures were adopted, enabling animals to feed successfully in all parts of the tree. The fine branch niche

Fig. 18. Mean time spent feeding by an animal each day during each month, in each study group.


GROUP I
GROUP II
GROUP III
GROUP IV
MEAN NUMBER OF MINUTES PER DAY SPENT FEEDING
320
270
220
170
120
JAN
OCT
FEB
NOV
MAR
DEC
APR
JUL
MAY
AUG
JUN
JUL
MONTHS

(Ripley, 1970) was reached by grasping a cluster of twigs in each hand and foot with the body suspended below, the animal thus distributing its weight over a considerable area. (A further analysis of posture and substrate types is given in Section VI.)

Amount of time spent feeding each day. Figure 18 shows the mean time an animal spent feeding each day during each month. These results were calculated combining data from all the age/sex classes with the one exception of data on the juvenile in Group III during the wet season. In the southern groups, analysis showed that individual animals differed from each other in the amount of time which they spent feeding. A Kruskal-Wallis One-way Analysis of Variance showed that the juvenile in Group III fed for significantly longer each day in the wet season than did other animals in the two southern groups ($N=34$, $H=11.9381$, $p \leq .01$). When the data on the juvenile were excluded, no significant difference remained between the other results. Excluding these data, therefore, and combining data for the two groups in each area, there was a highly significant difference in the south between time spent feeding each day in the wet season and time spent feeding each day in the dry season (Mann-Whitney U Test $N_1=N_2=6$, $U=0$, $p \leq .004$). The animals fed for much shorter periods each day during the dry season. In the north the difference was not significant ($N_1=N_2=18$). Mean time spent feeding per day in the south during the wet season was 246 minutes, while in the dry season it was only 173 minutes. In the north, the equivalent figures were 268 minutes and 245 minutes. Thus, although not significantly different, the results from the north did suggest the same trend towards a decrease in time spent feeding in the dry season.

Comparing results from the north and south for each season, there was no significant difference during the wet season. In the dry season,

however, the southern groups fed significantly less (Mann-Whitney U Test, $N_1=N_2=6$, U=o, $p \leq .001$) than those in the north.

Seasonal, regional and local variations in species composition of diet

In the results presented below, time spent feeding is equated with quantity eaten. It should be noted, however, that time spent feeding can only be a very approximate measure of quantity eaten, because it is unlikely that feeding rates were constant either between or within food species.

Variations between regions. Regional variation in the species composition of each group's diet was largely, but not uniquely, due to differences in the composition of the two forests. Only two food species, Commiphora pervilleana and Rothmannia decaryi, were eaten in both study areas. However, the importance of these two species for the animals' diet varied regionally: C. pervilleana was eaten commonly by both northern groups, but in the south neither group spent more than 1% of total feeding time eating it. Contrarily, R. decaryi was eaten in quantity in the south, and rarely in the north; further, in the south animals ate only the green ripe fruit of this species whereas in the north animals ate only its large white flowers. Cedrelopsis grevei and Baudouinia fluggeiformis were the only other two species present in both study areas. The southern groups both spent over 1% of total feeding time eating C. grevei whereas neither northern group was ever seen eating it, and the reverse applied to B. fluggeiformis, which was an important dietary component in the north and untouched in the south.

Considering overall diversity of diet, that of the southern groups contained fewer species than that of the northern groups. In the course of the field study, Group I was observed feeding on 88 known different

food species (including 5 liana species), and Group II on 102 (including 5 liana species). In the south, Group III was seen to feed on 79 different food species (including 15 liana species) and Group IV on 65 (including 13 liana species). These are likely to be conservative estimates, since species which could not be definitely re-identified when fed upon more than once were grouped into an "unidentified" category rather than each individual tree scored as a different species. The apparently greater selectivity in the south was to some extent illusory. Selectivity is a measure of the extent to which animals choose their food from the spectrum of potential food material available. Since a total of 167 different tree species were identified in the vegetational analysis in the northern study area, and only 70 in the southern, the northern groups fed on 49% (Group I) and 58% (Group II) of all tree species (lianas are discounted from these estimates), where in the south Group III fed on 91% and Group IV on 74% of all tree species. Thus the two southern groups appeared to be proportionately less selective in their choice of food species from available tree species within the forest. However, even this cannot be assumed to be a meaningful assessment of selectivity: what is crucial is the abundance of species. In the south, for example, although the number of species might not be much smaller than in the north, the canopy might be made up almost exclusively of two or three species and this, rather than overall reduction of species diversity, might be the cause of the comparatively few species eaten by the animals in the south. The limited evidence available (see Section II) suggests that the relative abundance of tree species in each forest was analogous, with a few species occurring commonly and most occurring rarely. Thus in this instance, the reduced diversity of diet in the south was probably related to the reduced overall diversity of tree species. Animals were proportionately less selective in the south, and in this

TABLE 14: Food species eaten by each group, ranked according to time spent feeding on each. Species eaten for less than 1% of total time spent feeding are not included.

Group I		Rank	Group II	
Food species	Time spent*		Food species	Time spent*
Drypetes sp.No.18	12.4	1	Drypetes sp.No.18	11.7
Cedrelopsis sp.No.471	5.4	2	Cedrelopsis sp.No.471	8.9
Liana No. 215	5.3	3	Liana No. 13	4.5
Dead Wood	5.3	4	Commiphora pervilleana	4.4
Capurodendron microlobum	5.1	5	Bathiorhamnus louveli	3.9
Rheedia arenicola Jerm & Perr	4.5	6	Dead wood	3.9
Commiphora pervilleana	4.2	7	Rhopalocarpus similis	3.7
Liana No.312	4.0	8	Liana No.215	3.6
Liana No. 38	3.7	9	Liana No.38	3.1
Protorhus deflexa	3.4	10	Boscia sp.No.302	3.3
Liana No.36	3.3	11	Protorhus deflexa	2.4
Mundulea sp.No.64	2.9	12	Capurodendron microlobum	2.3
Liana sp. No.13	2.2	13	Mammea sp.No.5	2.2
Polyalthia sp.No.116	2.1	14	Liana sp.No.36	2.2
Cedrelopsis sp.No.123	1.5	15	Rheedia arenicola Jerm & Perr	2.1
Baudouinia fluggeiformis	1.5	16	Macphersonia gracilis	1.9

* Results are expressed as a percentage of total time spent feeding.

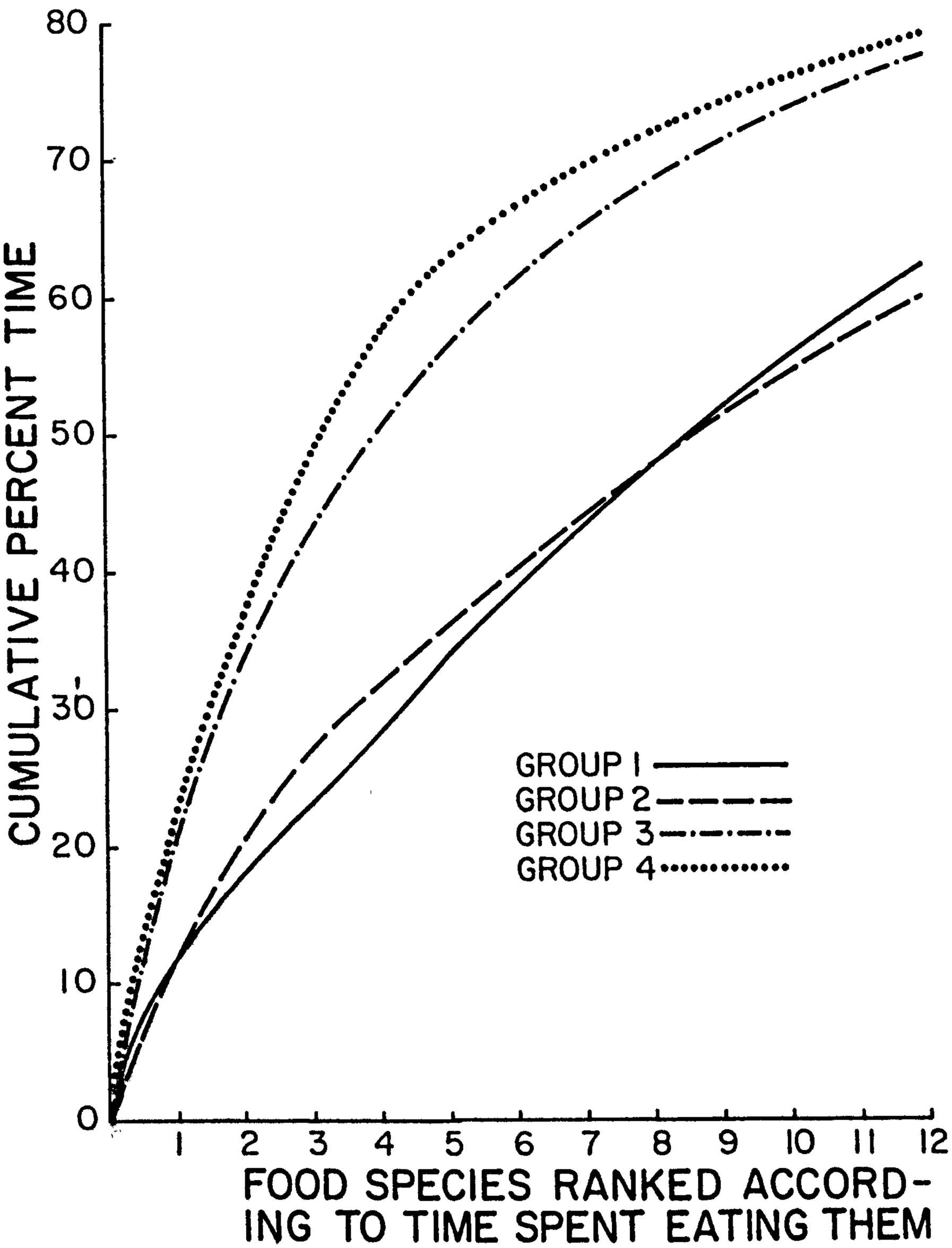
TABLE 14: Cont.

Group I		Rank	Group II	
Food species	Time spent		Food species	Time spent
Erythroxylon sp.No.514	1.5	17	Baudouinia fluggeiformis	1.8
Sp.No.433	1.5	18	Boscia sp.No.301	1.6
Boscia sp.No.301	1.5	19	Mimusops sp.No.320	1.6
Sp.No.211	1.4	20	Liana sp.No.296	1.6
Macphersonia gracilis	1.1	21	Holmskioldia microcalyx	1.3
Holmskioldia microcalyx	1.1	22	Sp.No.634	1.2
Liana No.452	1.1	23	Grewia sp.No.121	1.2
Mammea sp.No.5	1.1	24	Malleastrum sp.No.240	1.0
Boscia sp.No.302	1.1	25	-	
Boscia sp.No.603	1.0	26	-	
Group III			**Group IV**	
Terminalia sp.No.048	21.5	1	Terminalia sp.No.048	21.0
Mimosa sp.No.033	16.8	2	Liana sp.No.042	15.4
Liana No.042	12.3	3	Mimosa sp.No.033	11.2
Grewia sp.No.089	7.7	4	Grewia sp.No.059	9.9
Terminalia sp.No.09	5.0	5	Hagunta modesta	4.8
Diospyros Humbertii	4.1	6	Terminalia sp.No.09	4.3

TABLE 14: Cont.

Group III		Rank	Group IV	
Food species	Time spent		Food species	Time spent
Grewia sp.No.059	5.2	7	Grewia sp.No.089	2.6
Euphorbia plagiantha	2.3	8	Liana sp.No.053	2.5
Liana sp.No.054	2.1	9	Diospyros humbertii	1.9
Liana sp.No.053	1.9	10	Rothmannia decaryi	1.6
Hagunta modesta	1.8	11	Commiphora sp.No.092	1.6
Liana sp.No.056	1.7	12	Grewia sp.No.0126	1.5
Sp.No.0113	1.4	13	Liana sp.No.0125	1.5
Liana sp.No.058	1.3	14	Entada abyssinicus	1.4
Cedrelopsis grevei	1.3	15	Liana sp.No.054	1.4
Operculicarya decaryia	1.2	16	Cedrelopsis grevei	1.0
Liana sp.No.0146	1.1	17	Albizzia sp.No.034	1.0
-		18	Commiphora sp.No.076	1.0

Fig. 19. Overall amount of time each group spent feeding on the twelve food species eaten more commonly by each group than any other food species.


CUMULATIVE PERCENT TIME
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
GROUP 1
GROUP 2
GROUP 3
GROUP 4
FOOD SPECIES RANKED ACCORDING TO TIME SPENT EATING THEM

way they maximized the diversity of their diet.

Table 14 lists the food species on which each group spent a minimum of 1% of its total time spent feeding throughout the field study, ranked according to the time spent feeding on each. Group I, in the north, spent a minimum of 1% of total feeding time eating 26 different food species, and Group II 24. Group III, in the south, spent a minimum of 1% of total feeding time eating 17 species and Group IV 18. This again shows the wider diversity of diet of the two northern groups.

The two southern groups spent a much greater percentage of their total feeding time eating relatively few food species than did the northern groups. Figure 19 shows the amount of time each group spent feeding on the twelve food species eaten more commonly by each group than any other food species. These species were ranked according to the time spent feeding on them, and the results expressed cumulatively. The difference between the two regions was highly significant (Kolmogorov-Smirnov Two-sample Test, N=12, K_d=29.1, $p \leq .01$). Comparing the groups in each region, there was no significant difference between the two northern groups. Between the southern groups there was a significant difference (Kolmogorov-Smirnov Two-sample Test, N=12, K_d=7.6, $p \leq .05$). In using these tests, it was assumed that the data collected on an animal during one day was independent of data collected on another animal the following day.

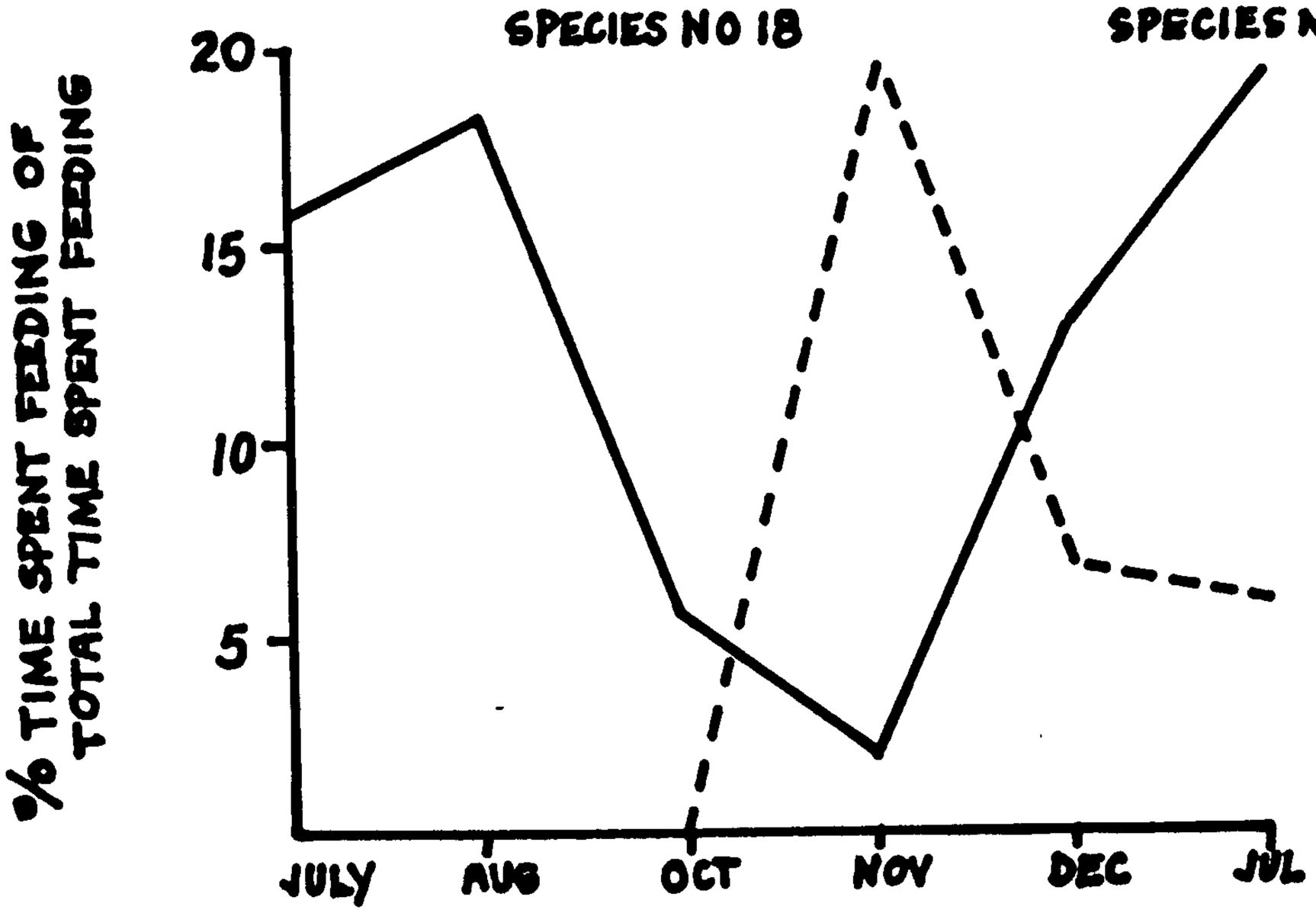
Variations between seasons. The composition of each group's diet changed almost completely between seasons. The figures in Table 14 represent the mean amount of time spent feeding on each food species throughout the field study, and give no indication of the variation in time spent feeding on each food species between months. Only five food species were eaten by the southern study groups for at least 1% each of total time spent

Fig. 20. Examples of monthly fluctuations in the importance of dietary components.

GROUP I

— Drypetes
SPECIES NO 18

--- Cedrelopsis
SPECIES NO 471



GROUP III

-.-.- Terminalia
SPECIES NO 048

..... Mimosa
SPECIES NO 083

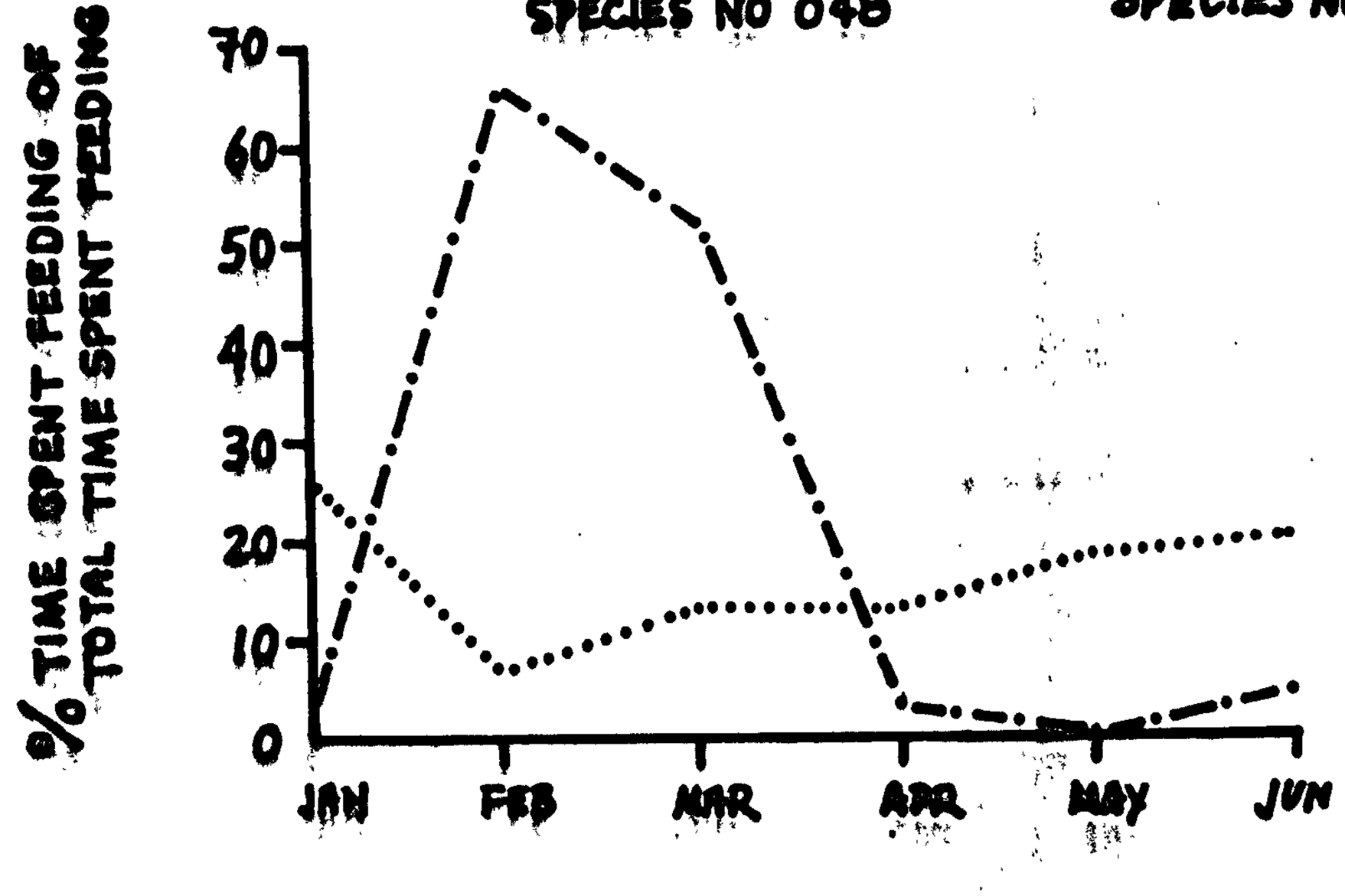


Fig. 21. Cumulative distribution of total feeding time between food species each month in Group 1.

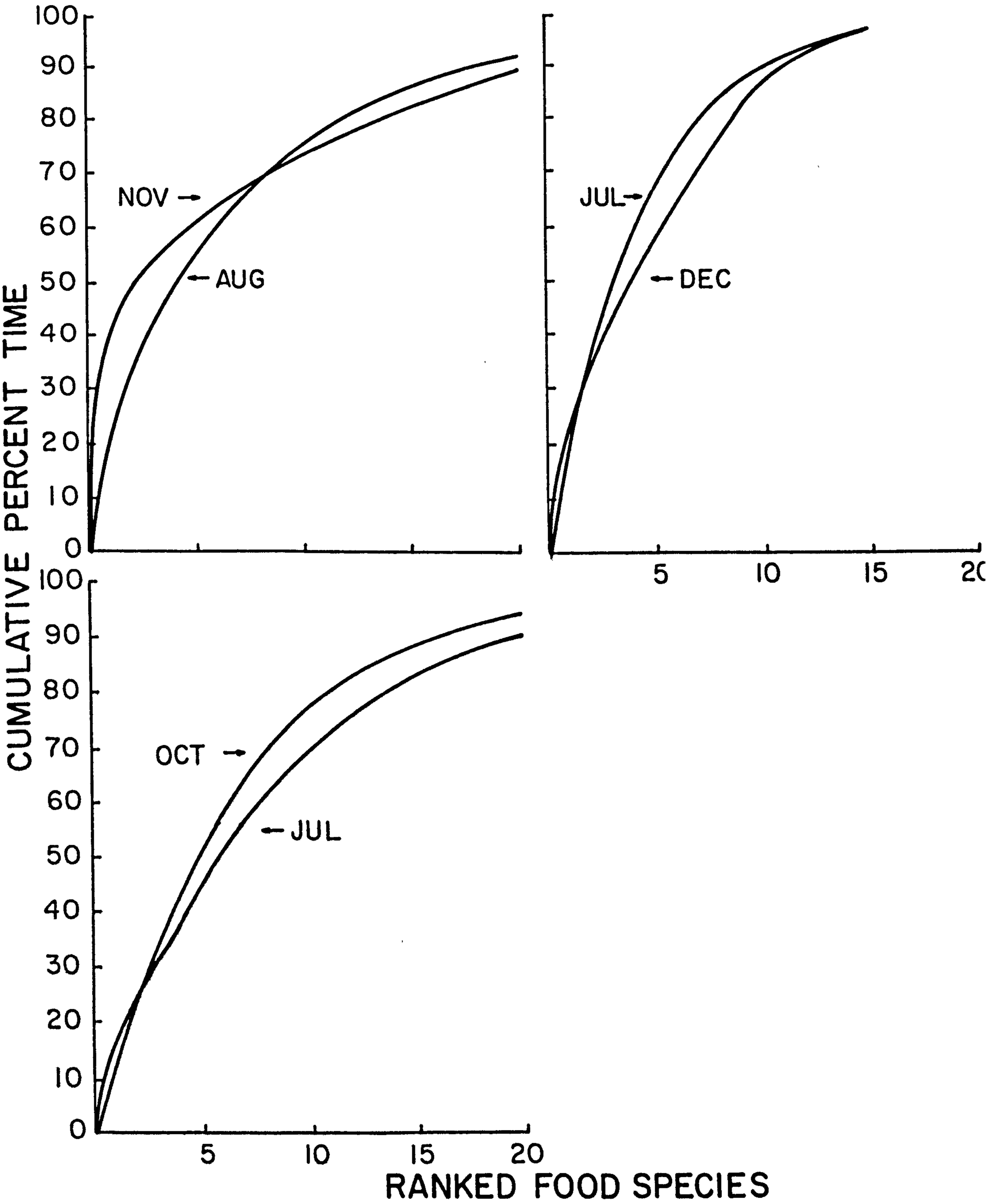

CUMULATIVE PERCENT TIME
100
90
80
70
60
50
40
30
20
10
0
NOV
AUG
JUL
DEC
OCT
JUL
5
10
15
20
RANKED FOOD SPECIES

Fig. 22. Cumulative distribution of total feeding time between food species each month in Group II.

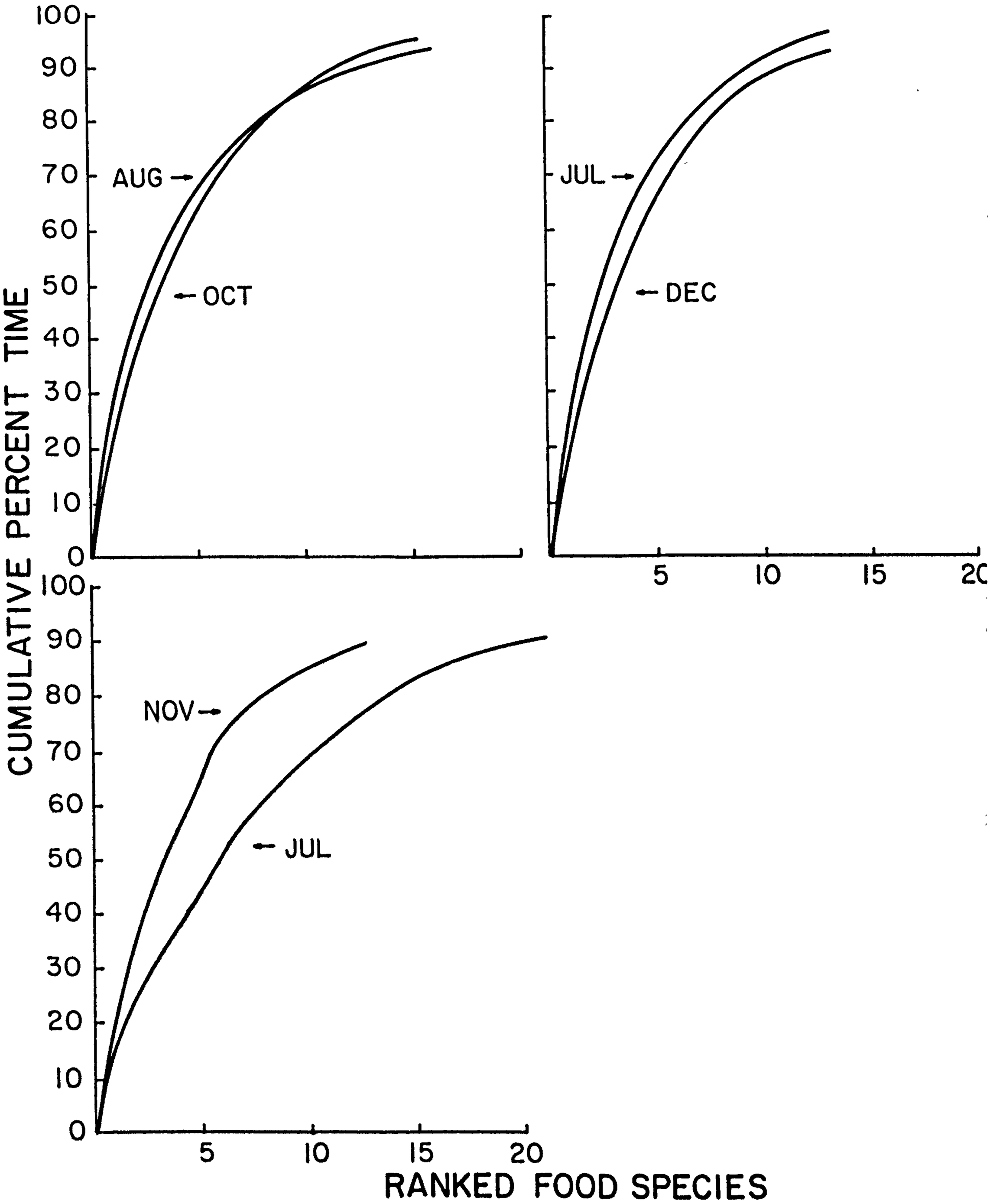

100
90
80
70
60
50
40
30
20
10
0
AUG
OCT
JUL
DEC
5
10
15
20
CUMULATIVE PERCENT TIME
NOV
JUL
RANKED FOOD SPECIES

Fig. 23. Cumulative distribution of total feeding time between food species each month in Group III.

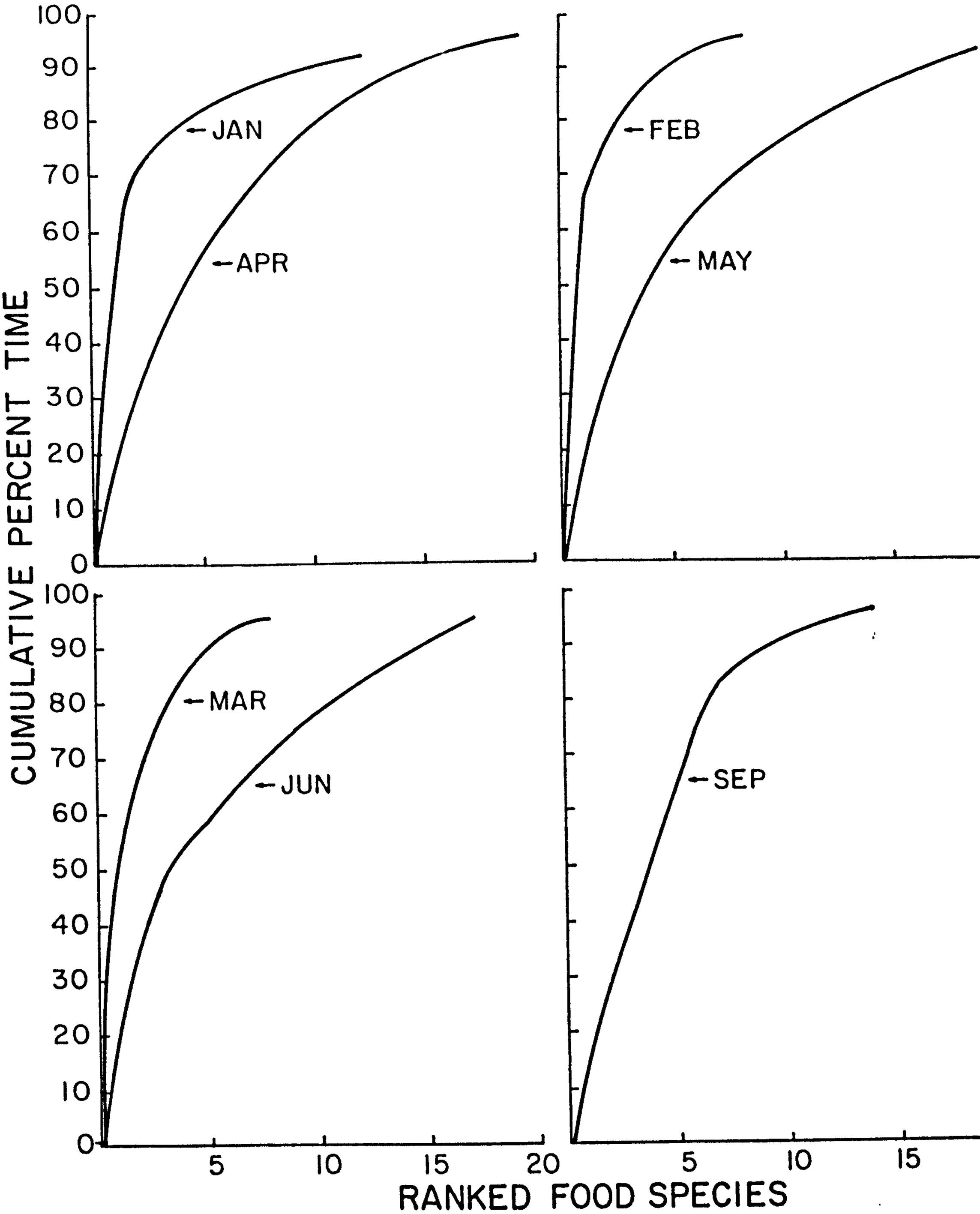

CUMULATIVE PERCENT TIME
100
90
80
70
60
50
40
30
20
10
0
JAN
APR
FEB
MAY
MAR
JUN
SEP
5
10
15
20
RANKED FOOD SPECIES

Fig. 24. Cumulative distribution of total feeding time between food species each month in Group IV.

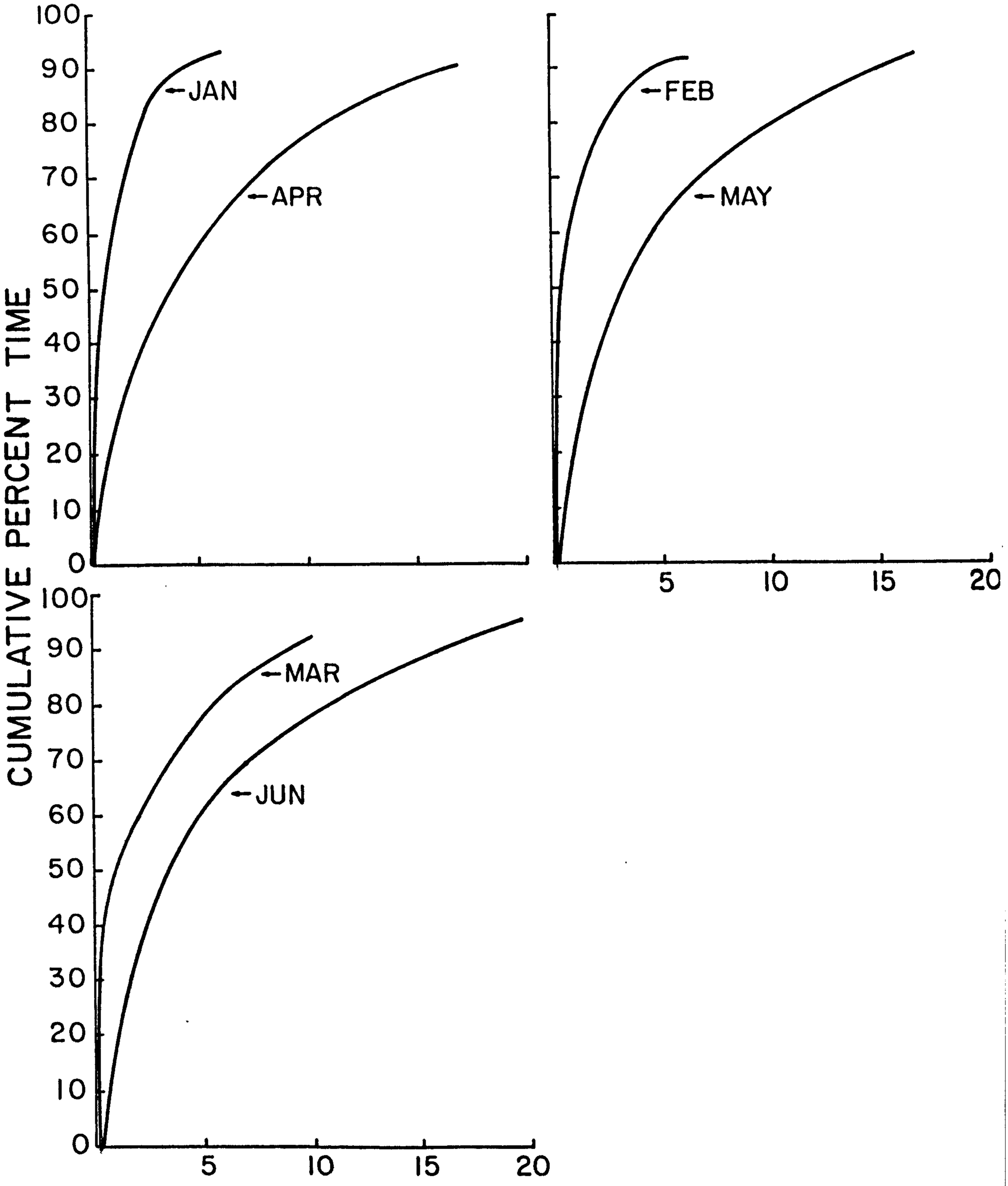

CUMULATIVE PERCENT TIME
100
90
80
70
60
50
40
30
20
10
0
JAN
APR
FEB
MAY
MAR
JUN
5
10
15
20
RANKED FOOD SPECIES

TABLE 15: Number of food species on which each group spent more than 1% of its total time spent feeding, in each season.

Month	No. of species		Month	No. of species	
	Group I	Group II		Group III	Group IV
July & August	18	22	May & June	18	19
Nov. & Dec.	13	17	Jan. & Feb.	8	6

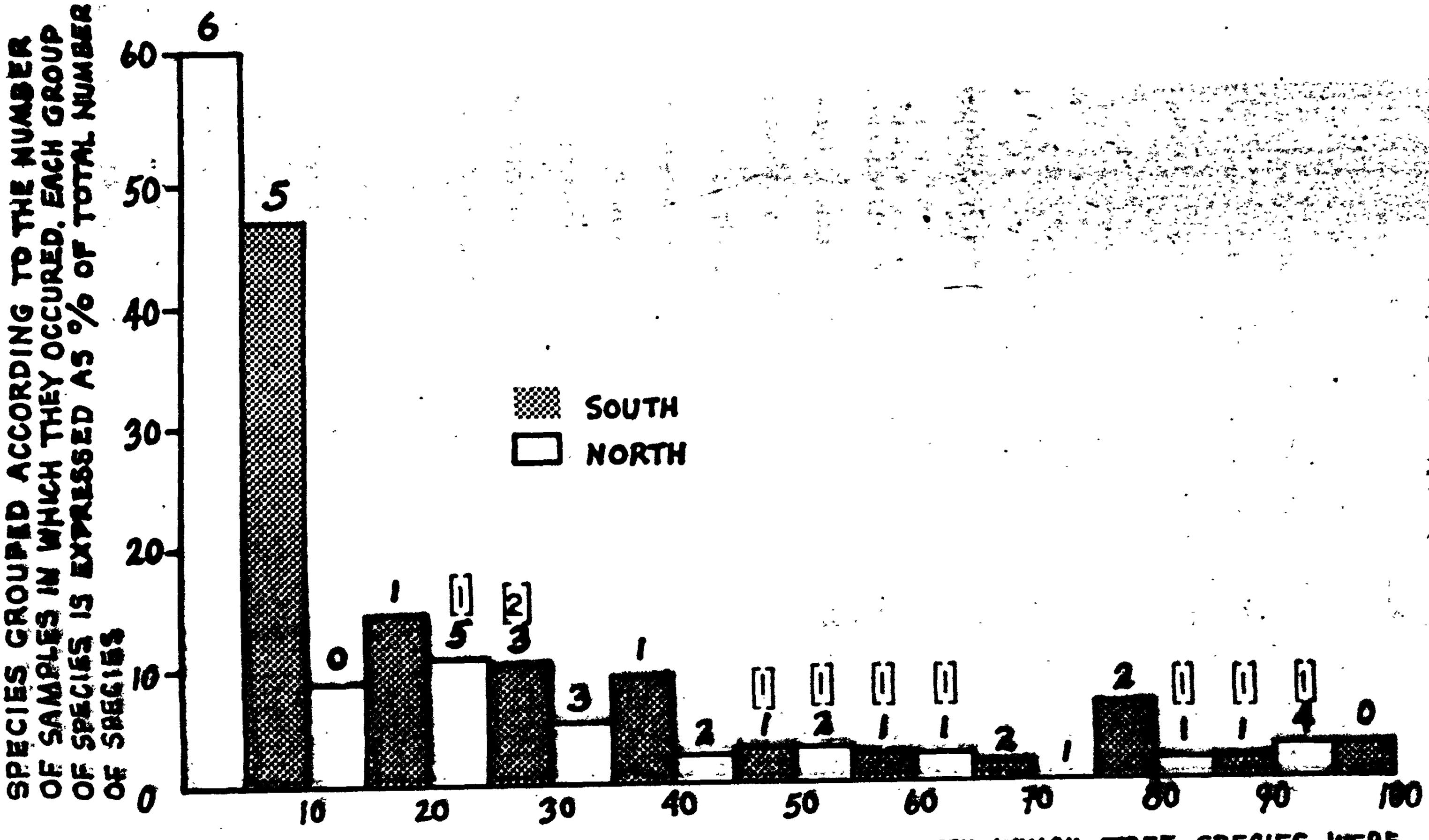
feeding in both the dry and wet seasons. The northern groups ate nine food species throughout the study. Figure 20 plots the percentage of total feeding time per month spent by Groups I and III feeding on the two food species that were most commonly eaten by each group in the course of the study. In both groups, one of these species - Drypetes sp. No. 18 in the north, and Mimosa sp. No. 033 in the south - was an important dietary item throughout the study; in contrast, the second species in both groups - Cedrelopsis sp. No. 471 in the north, and Terminalia sp. No. 048 in the south - constituted the bulk of the group's diet during a short period, apart from which it played little or no part in the group's diet. Similarly, food species which were each eaten for less than 1% of all feeding time throughout the study might be eaten for up to 5.9% of total feeding time in any one month and not be fed upon at all in any other month. This was true of a species of Croton, for example, which was eaten for 5.8% of total feeding time in January, by Group III, but no animal was observed eating it in any other month.

There were also marked seasonal differences in the diversity of diet of the two southern groups. Figures 21, 22, 23, and 24 express cumulatively the distribution of total feeding time between food species each month. In all cases a wet season month is plotted against a dry season month. In the north there was no consistent difference between the two seasons when all food species are considered. This contrasts with the situation in the south, where both groups in all cases fed more on fewer species in the wet season. At that time, between 80% and 90% of feeding time was generally spent on only five different food species.

If only food species on which each group spent more than 1% of total feeding time are considered, seasonal differences emerge in the northern, as well as the southern, groups. Table 15 lists the number of species on which each group spent more than 1% of total feeding time in four

months, two towards the end of the dry season, and two in the middle of the wet season. The contrast between the selectivity of the southern groups in the wet season and their catholicism in the dry season is clearer than that of the northern groups, but the difference between seasons in the number of food species on which each group spent more than 1% of its total feeding time each day was found to be highly significant in both areas (Mann-Whitney U Test, $N_1=N_2=12$, $U=3$, $p\leq.01$ - north; $N_1=N_2=12$, $U=0$, $p\leq.01$ - south).

Local variation. A certain amount of variation was seen between the diets of the two groups in each study area. Group I fed on 6 species of which 5 were eaten by Group II for less than 1% of feeding time, but Group II was never seen eating the sixth, Malleastrum sp. No. 240. Group II fed on 8 species of which 7 were eaten by Group I for less than 1% of total time spent feeding, but Group I was never seen eating the eighth, Erythroxylon sp. No. 514. In the south Group III fed on 7 species which were eaten by Group IV for less than 1% of total time spent feeding, and Group IV on 6. No single food species was eaten by one group and not the other in the south. In the north and south, eight out of twelve species most commonly fed on by each group were the same, and there was a highly significant correlation between the way the two groups in each area allotted feeding time to these species (Spearman Rank Correlation Coefficient, $N=24$, $r_s=.76$, $p\leq.01$ - south; $N=32$, $r_s=.53$, $p\leq.01$ - north). There was proportionately more variation between the diets of the two southern groups than those of the northern groups. 41% of the food species eaten for more than 1% each of total time spent feeding by Group III were eaten for less than 1% each of total time spent feeding by Group IV, and 33% of the food species eaten for more than 1% each of total time spent feeding by Group IV were eaten for less than 1% each of



FREQUENCY, EXPRESSED AS A PERCENTAGE, WITH WHICH TREE SPECIES WERE PRESENT IN SAMPLE CIRCLES.

total time spent feeding by Group III. Equivalent values for Groups I and II were 23% and 33%.

This variation between the diets of adjacent groups may be due to various factors. "Cultural" differences between groups may result in group-specific differences in the choice of certain preferred food species. It is also possible that differences in the species composition of each group's home-range may result in local variations in the availability of certain foods, and hence in slight variations in diet.

Abundance of food sources

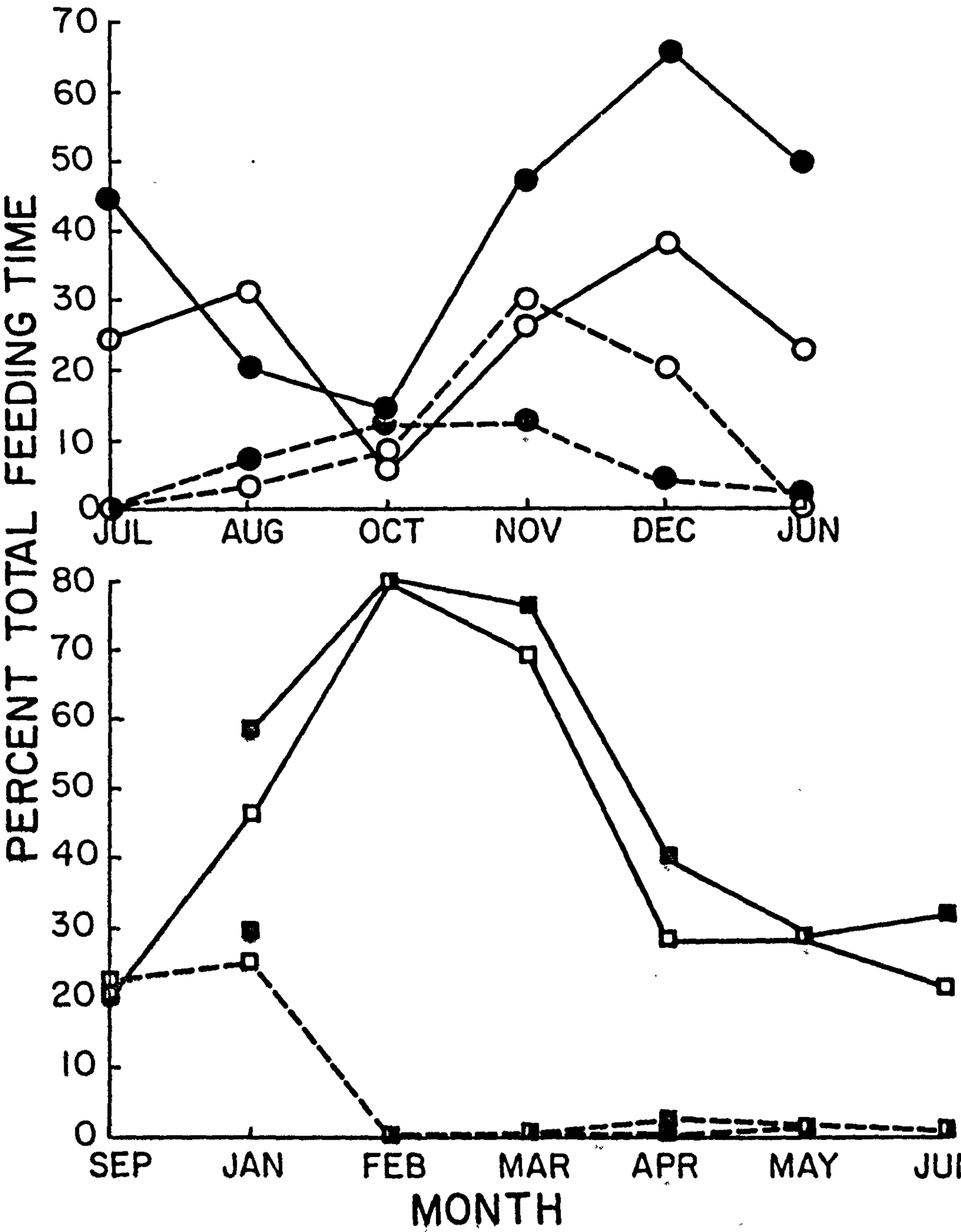
The availability of food sources may be an important factor in determining home-range size. Data from the analysis of the vegetation in each study area (see Section II) were used to provide a rough assessment of the availability of the various components of the study groups' diets. The total abundance of tree species in the vegetational samples was closely related to the frequency with which they were recorded as present or absent in these samples (see P.116), and frequency of occurrence is here considered as a measure of abundance.

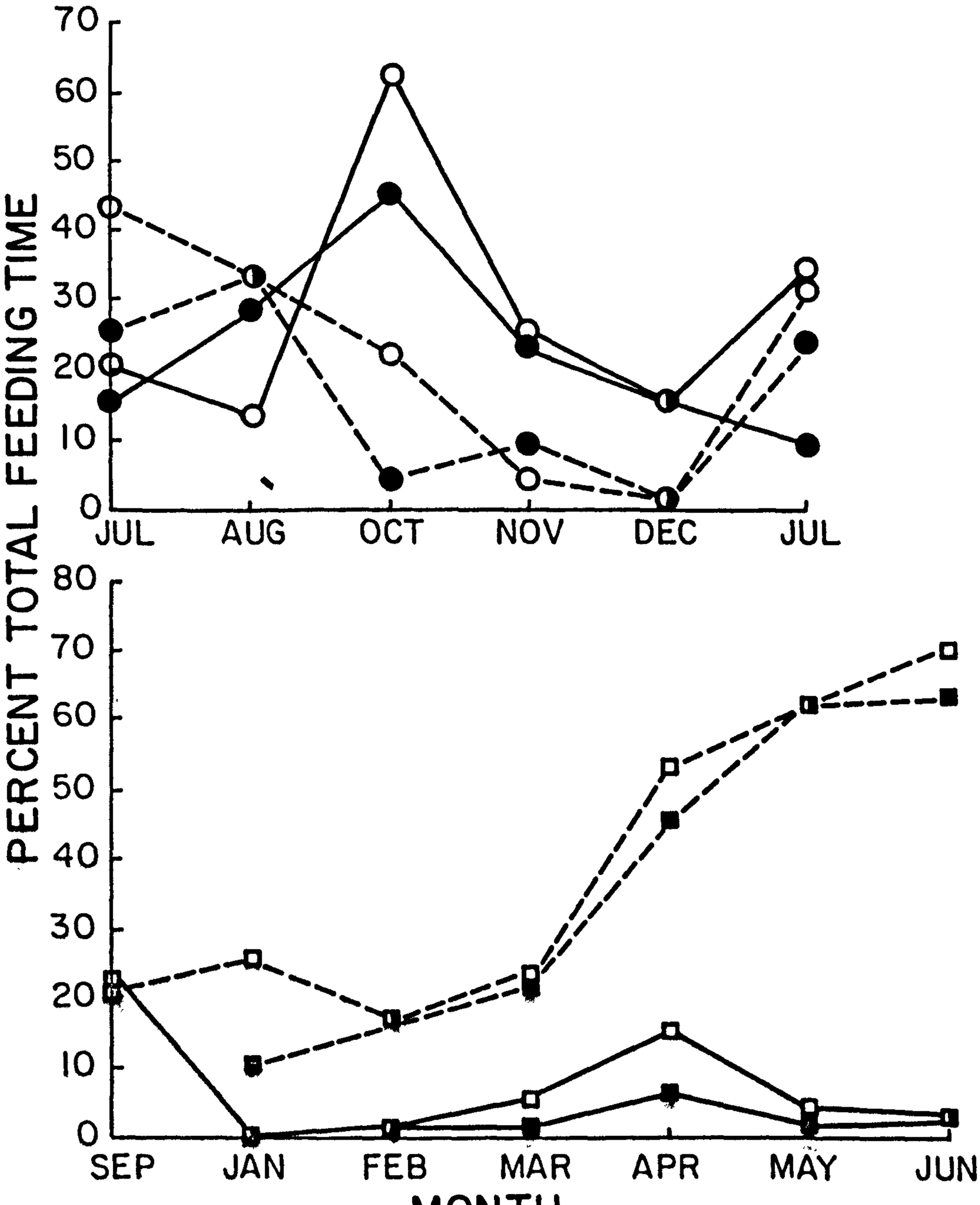
In both areas groups ate a high number of food species which occurred frequently in the forest, instead of seeking out more rarely occurring tree species. Figure 25 shows again tree species grouped according to the frequency with which they were present in sample circles of the vegetational analysis. The figures without brackets indicate the number of food species coming from each group of tree species that was eaten by any of the four study groups for more than 1% of total feeding time. It is apparent that right across the spectrum, from rarely occurring to commonly occurring species, there were species that provided food for one or both groups in each area. However, proportionately, there was an imbalance: in the north, 87% of the total number of tree species identified

occurred in less than half the total number of sample circles, yet only 64% of Groups I and II's food species came from these species, and the remaining 36% from the 13% of tree species that occurred in more than half the sample circles. The situation in the south was remarkably similar: 84.5% of the total number of tree species occurred in less than half the circles, and yet they constituted only 65% of the total number of food species of Groups III and IV. The remaining 35% of food species came from the 15.5% of the total number of tree species which occurred in more than half the sample circles.

Despite this imbalance, it should be noted that rarely occurring tree species did constitute almost two-thirds of the total number of food species. Separate analysis of feeding data from wet and dry season months showed that this was equally true in both seasons.

Since the amount of time spent feeding on species differed widely between species it cannot be assumed that the analysis above gives an accurate picture of the abundance of the major part of the groups' food supplies. The numbers in brackets in Figure 25 indicate the number of Groups I and III's first five food species (excluding lianas), ranked according to time spent eating them, coming from each group of tree species. Group I spent 31.6% of total feeding time eating these species, and Group III 55.1%. The distribution of the results shows that even among the groups' most commonly eaten foods there was a wide range of variation in the abundance of the food species. Although not as wide as that when all food species eaten for more than 1% of feeding time are considered, the variation was still sufficient to indicate that the animals did not necessarily rely heavily on abundant tree species as food sources.


PERCENT TOTAL FEEDING TIME
70
60
50
40
30
20
10
0
JUL
AUG
OCT
NOV
DEC
JUN
80
70
60
50
40
30
20
10
0
SEP
JAN
FEB
MAR
APR
MAY
JUN
MONTH
GROUP 1 O GROUP2 ● GROUP 3 □ GROUP 4 ■
FRUIT ——— FLOWERS - - - - -


PERCENT TOTAL FEEDING TIME
70
60
50
40
30
20
10
0
JUL
AUG
OCT
NOV
DEC
JUL
80
70
60
50
40
30
20
10
0
SEP
JAN
FEB
MAR
APR
MAY
JUN
MONTH
GROUP 1 O GROUP 2 ● GROUP 3 □ GROUP 4 ■
YOUNG LEAVES—— ADULT LEAVES— — —

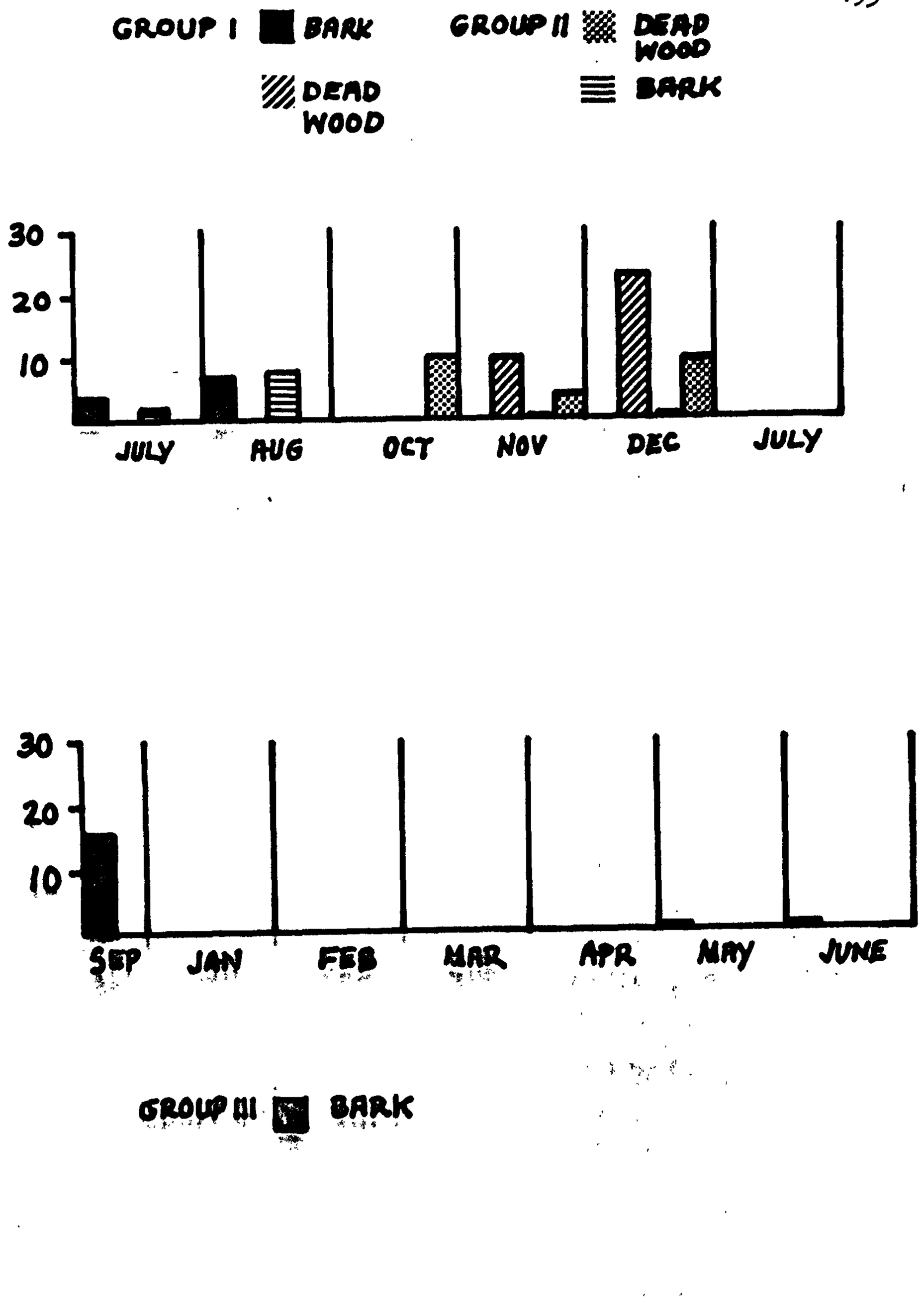
Seasonal variations in food part eaten

There were consistent seasonal and regional differences in the parts eaten of trees and lianas, irrespective of species. This variation was related to changes in the phenology of tree species and, indirectly, to seasonal/climatic factors.

Figure 26 shows the percentage of total feeding time which each group spent eating fruit, flowers and flower buds. Figure 27 shows the percentage of total feeding time which each spent eating leaflets, shoots, young leaves, flush and buds, and adult leaves. (Definitions of these phenological categories were given in Section II.) Data on Group III for September 1970 are included.

The high figure for flowers in the south during the month of September is a reflection of the phenological state of Alluaudia ascendens and Alluaudia procera. Both these species flowered at this time, and their flowers constituted a large part of the diet of Group III and all of the "22% flowers" category in Figure 26 (c.f. Charles-Dominique and Hladik, 1971). In January, flowers were an important dietary item for both Groups III and IV, but for the rest of the wet season fruit constituted an overwhelming proportion of their diet. At the onset of the dry season there was an increase in the amount of time spent feeding on adult leaves, and this continued to increase through the dry season until the end of the study in June. Comparing the situation in June with that in the preceding September, the contribution of fruit to the diet of Group III was approximately equal; the significance of the high "Flowers" result has already been mentioned. A higher proportion of the diet was made up of young leaves in September than at any other time, however. In June, young leaves constituted less than 5% of the diet of either group. The ability of individual trees in the south to produce young leaves at

Fig. 28. Percentage of total feeding time which each group spent eating bark and dead wood.


GROUP I
BARK
DEAD WOOD
GROUP II
DEAD WOOD
BARK
30
20
10
JULY
AUG
OCT
NOV
DEC
JULY
30
20
10
SEP
JAN
FEB
MAR
APR
MAY
JUNE
GROUP III
BARK

intervals well into the dry season was documented in Section I. It is suggested that three freak showers of rain at the beginning of September were sufficient to lead to the production of leaf shoots by many individuals from many species simultaneously, and that Group III profited from this.

In the north, a general peak in young leaf consumption occurred at the same time as a decrease in adult leaf consumption at the beginning of the wet season. Further into the wet season, consumption of young leaves declined too, and there was an increase in the consumption of flowers in November, followed by a large increase in time spent feeding on fruit in December. At that time, 65% of Group II's feeding time was spent eating fruit, and 39% of Group I's. There was a general decrease in time spent feeding on fruit and flowers in the dry season, and a general increase in time spent feeding on adult leaves. Time spent feeding on young leaves decreased generally, as might be expected, in the dry season, but the result for Group I, July 1971, did not conform to this pattern: a large proportion of the time this group spent feeding on young leaves was spent in a single tree of Capurodendron microlobum which was covered with leaf buds at that time. Subjective impressions and data from Section II on synchrony suggest that budding occurred abnormally and uniquely in this one tree.

Bark and dead wood as dietary components

A high proportion of time was spent feeding on bark and/or dead wood by the study groups at certain times of year. Figure 28 shows the amount of time each group spent feeding on these materials each month. In the south, no animal was ever seen eating dead wood, but during the last six weeks of the study, animals in Group III were seen feeding briefly on

the bark and cambium of Operculicarya decaryi. In the previous September, however, they had spent 15.5% of their total feeding time eating the bark and cambium of this species. Animals gouged out the relatively soft wood with its skin-like bark with their "tooth-combs," leaving scars on the tree trunk up to 1cm. deep and 4cm. long. Each mouthful was chewed up using the molars and premolars. A piece of this wood weighing 37.75g. immediately after being cut from the trunk in September 1970 finally stabilized at 7.25g. after drying for two weeks. It therefore contained 81% water by weight. Another piece, cut the following September in the same area weighed 48.1g., and 12.75g. after drying, thus containing 74% water by weight. Evidently, this species might serve as a most important source of water at the end of the dry season.

In the north, both groups ate bark to the exclusion of dead wood in the dry season, and dead wood almost to the exclusion of bark in the wet season. The bark eaten in the dry season came mainly from thin branches of Commiphora pervilleana; the bark alone was stripped off, using first the "tooth-comb" to prise up the bark and then the premolars to tear it off. The underlying wood was not gouged out as in the south. The bark appeared to contain little water and was probably eaten for its nutritive value rather than as a source of water (see Plate XIII).

The functional role of dead wood in the diet of the northern groups is more difficult to understand. In the wet season, it was a major item in the diet of both groups. Each group would cluster round a tree trunk lying on the ground, or an upright, lightening-blasted one, and tear off splinters of wood using "tooth-combs" and premolars. Each group used two hunks of dead wood within their home-range in this way. Further dead trunks were present in both home-ranges of both groups which did not differ noticeably from those used as food sources, but they were not touched,

and the trunks on which animals fed during the field study looked as if they had been used over a period of years. During the eighteen-month study, the effect of the groups on the appearance of these trunks was negligible, yet all showed deep, smoothly worn indentations at the beginning of the study. It is possible that another species of lemur, or a carnivore, was also using these trunks although no evidence for this was found. Close examination of the wood did not reveal any signs of bore holes made by insect larvae: it appeared, rather, to be very dry, very hard, and very dense.

The rate of food consumption was low when animals ate this wood in that they appeared to have considerable difficulty in tearing off mouthfuls, so that the time spent feeding on dead wood probably over-emphasized its real dietary value (see also P. 162). Nevertheless, in both northern groups it ranked very highly in order of time spent feeding (see Table 14) and must presumably have had considerable significance for the diet of the animals studied. The nature of the significance is not understood.

DISCUSSION AND CONCLUSIONS

Two main issues emerge for discussion: the reasons underlying the dramatic seasonal change in feeding and ranging behaviour in both study areas, and the causes and function of the difference in group dispersion. The latter was the only factor in which there seemed to be a regional difference of "kind" rather than degree.

Variations in feeding and ranging behaviour

The quantitative differences in most aspects of ranging and feeding behaviour were greater between seasons within each area than between the two areas, and such differences as were found between the two areas seemed largely to be a reflection of the more pronounced seasonality of the

southern study area. In the dry season in both study areas, animals moved short distances each day and fed for short periods on a wide variety of food species. In the wet season, they moved much further each day and fed for much longer periods on fewer species. Although in the wet season all groups entered more squares of the grid in a given time period than during the dry season, there was no evidence to suggest that a significant expansion of home-range size took place. The difference of "degree" referred to above, is found throughout the data. For example, Figure 18 indicated that there was a slight drop in time spent feeding per day by the two northern groups in the dry season, although in fact the difference was not statistically significant. Results for the southern group showed a considerable drop, and the difference between the two seasons was highly significant. Similarly, there was a greater difference in the south in the daily distance moved, between each season, than there was in the north.

In view of the absence of data on the primary productivity of each forest, the nutritive value of food species and the energy budget of P. verreauxi, possible explanations of the causes of the regional and seasonal differences can be little more than speculation. However, I believe that they can be tentatively traced to changes in food availability and distribution, and to changing thermo-regulatory requirements. The latter are discussed in Section VI, and only food sources are considered here.

In Section II, results indicated a greater overall diversity of tree species in the northern forest, and more dense vegetation in general, although there appeared to be a similar degree of inter- and intra-specific synchrony between trees in each forest. The wider diversity of diet of the two northern groups reflected this diversity of tree species, although in proportion to the number of tree species present they ate relatively

fewer food species than the southern groups. It is possible that primary productivity was greater in the north than in the south, and probable that in both study areas it was greater in the wet season than in the dry. If the decrease in productivity resulted in a general decrease in food availability in the dry season, particularly in the southern study area, then it is possible that because of this overall decrease animals fed less, consequently had less net energy and, as a result of this, moved less. If levels of food availability did not decline as far in the northern study area as in the south, one would predict the similar, but less extreme, behavioural changes that were in fact observed in the north. However, primary productivity cannot <u>per se</u> be equated with food availability for a given animal species without ignoring the selectivity exercised by that animal species with reference to food, so this argument rests on a dubious premise.

Alternatively, it is possible that seasonal changes in ranging patterns may have been partly due to changes in the components of the diet of the animals studied. Such changes were probably related both to variation in the availability of food sources, including their size and distribution, and to changes in the degree of selectivity exercised by the animals. In the wet season in both areas, the young leaves, fruit and flowers of a relatively few tree and liana species constituted a major part of the study groups' diet. In the dry season, animals fed mainly on the adult leaves of many species. The seasonal change in the type and range of food available, and the associated increase in selectivity may have been a contributing cause of the increased distances travelled in the wet season. It has been shown that, in both seasons, over 50% of food species were, according to the vegetational analysis, quite rarely occurring, and also that tree species tended to be widely scattered through both forests rather than evenly distributed. It is

possible the more selective the animals were and, thus, the more restricted their diet became, the further they had to move in order to find sufficient quantities of the selected food species. Further, it is probable that there was less food available at each individual food source in the wet season, because the animals were eating fruit rather than adult leaves.

The increase in time spent feeding may have been related to a number of factors. It could be argued that animals had to feed longer each day in order to build up sufficient energy for the longer daily ranging patterns. This is unlikely, however, since the nutritive value of the young leaves, flowers and fruits of the wet season was probably much higher than that of the adult leaves of the dry season (Golley, 1961; Hladik et al., 1971), suggesting that animals would need to spend less time feeding in the wet season. It is possible that more time was spent feeding because feeding rates were lower, reduced by the less dense nature of the food source. Finally, animals may have been undergoing a net gain in energy during the early part of the wet season, in preparation for the great energy expenditure of the mating season (see Section VIII) which occurred towards the end of the wet season.

In summary, the data collected on the animals and in the course of the vegetational analysis support the hypothesis that changing levels of food availability, and changes in the degree of selectivity and the type of food chosen, may produce seasonal variation in feeding and ranging patterns. At the same time, these factors are unlikely to have been the only ones involved, and other aspects of the observed seasonal variation are discussed elsewhere.

Group dispersion

Three contrasting situations were found with reference to home-range size and the maintenance of its exclusivity. In the northern study area home-range size was approximately equal to that in the south, but the home-ranges of both groups studied overlapped extensively with those of other groups. Inter-group encounters occurred throughout these areas of overlap, and monopolized zones were widely scattered. In the south, overlap between groups' ranges was minimal, and inter-group encounters took place only in the narrow overlap strips (except in the mating season - see Section VIII). One extensive monopolized zone was located in the middle of each home-range. Thirdly, Jolly (1966) described home-ranges of P. verreauxi at Berenty about one quarter the size of those described in the present study, but with proportional overlap between the groups almost identical to that found in the southern study area in the present study. She also described her study groups as having a "nucleus of territory that others did not penetrate" and suggested that "the territory and range of a group represent some minimum combination of behavioural-ecological requirements." Petter (1962a) likewise commented that P. verreauxi territories varied in size, being large where the forest was sparse and small where it was thick.

If the situation in the northern study area is assumed to be normal, rather than temporary and aberrant, then this argument that all groups possess a central territory, whose size varies from area to area, is no longer tenable. A functional interpretation of the differences can be made in the light of the differing ecological conditions present in each of the three regions. The evidence did not indicate seasonal fluctuations in home-range size, but rather in the rate at which that home-range was traversed; thus it is probable that each group foraged

over, and was familiar with, a total home-range large enough to provide food for the group throughout the year. It has been shown that in both areas most food species were eaten seasonally rather than throughout the year and, further, that many food species occurred rarely in each forest. The low stature of both the northern and southern forests was described in Section II. These factors together indicate that in both study areas the individual trees constituting a given food species were often likely to be not only widely scattered but also relatively small.

It is on the basis of the above observations that the following hypothesis is put forward. In the north, each group required its total home-range in the course of a whole year, because of the varying distribution and small size of important, but scattered foods; at any one time, however, the total food available within the home-range was in excess of the group's immediate requirements and overlap between groups could be extensive. It is likely that the scattered, so-called "monopolized" zones were simply areas where I did not see other groups, rather than areas where other groups did not go. The avoiding action generally taken when groups met probably increased group dispersion. True "battles," as described by Jolly (1966) almost always occurred at a major food source which one or the other group was feeding on immediately before the encounter. This would be expected in a system where minimum home-range size is determined not by total food availability but by the distribution of a few important food sources. In the south, I believe that towards the end of the dry season food did become a critical, limiting factor, and that at this time the whole home-range was necessary to support one group. The round-the-year territoriality found in the south may be an adaptive response to this minimum foraging area requirement that operates at times of greatly reduced food availability. At

TABLE 16: The relationship between dispersion and size of food source, and home-range size and overlap between groups, based on data from Ampijoroa, Berenty and Hazafotsy.

Area	Distribution and size of food sources	Food availability within home-range	Home-range size	Degree of overlap
Ampijoroa (northern study area)	Major food sources widely scattered and small	In excess of group's requirements at any given time	large	extensive
Berenty	Major food sources concentrated and large	Probably in excess of group's requirements at any given time	small	minimal
Hazafotsy (southern study area)	Major food sources widely scattered and small	Becomes limiting factor during critical periods e.g. drought	large	minimal

Berenty, the kily trees provided a huge, almost continual food source for P. verreauxi (see Jolly, 1966). I agree with Jolly that in this area of high population density, behavioural as well as ecological requirements are probably determinative of home-range size and exclusivity. It is possible that crowding rather than food may be a limiting factor in this reserve, for the large, closely concentrated food sources may permit a theoretical reduction of home-range size per group beyond that compatible with behavioural requirements.

The relationships between the dispersion and size of food sources on the one hand, and home-range size and degree of overlap between the groups on the other, formulated on the basis of data collected in this and Jolly's study, are summarized in Table 16.

Determination of the basis of these differences between the two populations of P. v. verreauxi and one of P. v. coquereli is a complex problem which cannot be resolved here. As suggested above, it is very likely that ecological parameters were, at least in part, determinative of the observed variation. It is also possible that genetic differentiation between the two sub-species may have contributed to the behavioural variation: indeed, there could conceivably be a genetically based tendency towards territoriality in P. v. verreauxi which was absent in P. v. coquereli. However, even if this is true, genetic differentiation must have occurred in response to different environmental pressures and functional interpretations should still be sought.

SUMMARY

1) This Section describes the general characteristics of feeding behaviour in the groups of P. verreauxi studied. An animal was said to be feeding when it was chewing the bark, buds, leaves, flowers or fruit of a plant species. No analysis of foraging behaviour was made

because of the probable inaccuracy of the data.

2) In the wet season, all groups tended to have two feeding bouts, one in the morning and one in the afternoon. In the dry season, there was one main feeding bout which reached a peak towards midday.

3) Both feeding rates and inter-animal distance varied considerably in the course of feeding bouts.

4) Many feeding postures were adopted, enabling animals to feed successfully in most parts of the tree.

5) In the south, individual animals differed from each other in the mean amount of time they spent feeding each day: the juvenile in Group III fed for longer each day in the wet season than did other animals in that group.

6) Animals in the south fed for much shorter periods each day during the dry season than in the wet. The results from the north suggested a similar, but less pronounced trend.

7) Regional variation in the species composition of each group's diet was largely, but not uniquely, due to differences in the composition of the two forests. Only two food species were eaten in both study areas, but both the part eaten and the amount of time spent eating varied. Two other tree species were found in both forests; both were eaten in one of the two forests, but neither was eaten in both forests.

8) The diet of the southern groups contained fewer species than that of the northern groups. The apparently greater selectivity of the southern groups was to some extent illusory, however: fewer tree species were present in the southern forest, and animals fed on a proportionately wider range of them than in the north. Thus the southern groups were proportionately less selective, and in this way they maximized the diversity of their diet. Associated with this difference, the two southern groups spent a much greater percentage of their total feeding

time eating relatively few food species than did the northern groups.

9) The composition of each group's diet changed almost completely between seasons. There were also marked seasonal differences in the diversity of diet of the two southern groups: both groups fed more on fewer species in the wet season. There was no consistent difference in this respect between the two seasons in the north. However, if only food species on which each group spent more than 1% of total feeding time are considered, seasonal differences emerge in the north also, with greater diversity of diet being present in the dry season.

10) A certain amount of variation was seen between the diets of the two groups in each study area. There was proportionately more variation between the diets of the two southern groups than those of the northern groups. This variation may be due to differences in food availability between home-ranges, or to group-specific variation in preferred foods.

11) The availability of food sources may be an important factor in determining home-range size. In both areas groups ate a proportionately high number of food species which occurred frequently in the forest, although rarely occurring tree species did constitute almost two-thirds of the total number of food species. Even among the groups' most commonly eaten foods there was a wide range of variation in the abundance of the food species.

12) There were consistent seasonal and regional differences in the parts eaten of trees and lianas, irrespective of species. This variation was related to changes in the phenology of tree species and, indirectly, to seasonal/climatic factors.

13) A high proportion of time was spent feeding on bark and/or dead wood by the study groups at certain times of year. In the south, no animal was ever seen eating dead wood, but bark was eaten in the dry season. This may have been an important source of water during the dry

season. In the north, animals ate bark to the exclusion of dead wood in the dry season, and dead wood almost to the exclusion of bark in the wet season. The functional role of dead wood in the diet of the northern groups was not understood.

14) The quantitative differences in most aspects of ranging and feeding behaviour were greater between seasons within each area than between the two areas, and such differences as were found between the two areas seemed largely to be a reflection of the more pronounced seasonality of the southern study area. In the dry season in both study areas, animals moved short distances each day and fed for short periods on a wide variety of food species. In the wet season, they moved further each day, and fed for longer on fewer species. It is possible that a decrease in primary productivity in the dry season resulted in a decrease in food availability, and that animals therefore fed less, consequently had less net energy, and thus moved less. Alternatively, it is possible that seasonal changes in ranging patterns may have been due to changes in the components of the diet of the animals studied. Such changes were probably related both to variation in the availability of food sources, including their size and distribution, and to changes in the degree of selectivity exercised by the animals. It is likely that the more selective the animals were and, thus, the more restricted their diet became, the further they had to move in order to find sufficient quantities of the selected food species.

15) In the north, home-ranges overlapped extensively, and monopolized zones were scattered through each group's home-range. In the south, home-range size was similar, but overlap between groups was minimal, and both study groups had exclusive use of the central part of their home-range. At Berenty, home-ranges were about one quarter the size of those described in the present study, with proportional overlap between the

groups almost identical to that found in the southern study area. It is postulated that in the north, each group required its total home-range in the course of a whole year, because of the varying distribution and small size of important, but scattered foods. At any one time, however, the total food available within the home-range was in excess of the group's immediate requirements and overlap between groups could be extensive. In the south, food probably became a critical limiting factor towards the end of the dry season, and at that time the whole home-range was necessary to support one group. The round-the-year territoriality found in the area may be an adaptive response to this minimum foraging area requirement that operates at times of greatly reduced food availability. At Berenty, as Jolly (1966) suggests, behavioural as well as ecological requirements are probably determinative of home-range size; in this area of high population density, crowding rather than food may be a limiting factor, for the large, closely concentrated food sources may permit theoretical reduction of home-range size per group beyond that compatible with behavioural requirements.

Fig. 29. Mean monthly precipitation, and mean number of days each month on which rain fell, in northern study area.

Fig. 30. Mean monthly precipitation, and mean number of days each month on which rain fell, in the southern study area

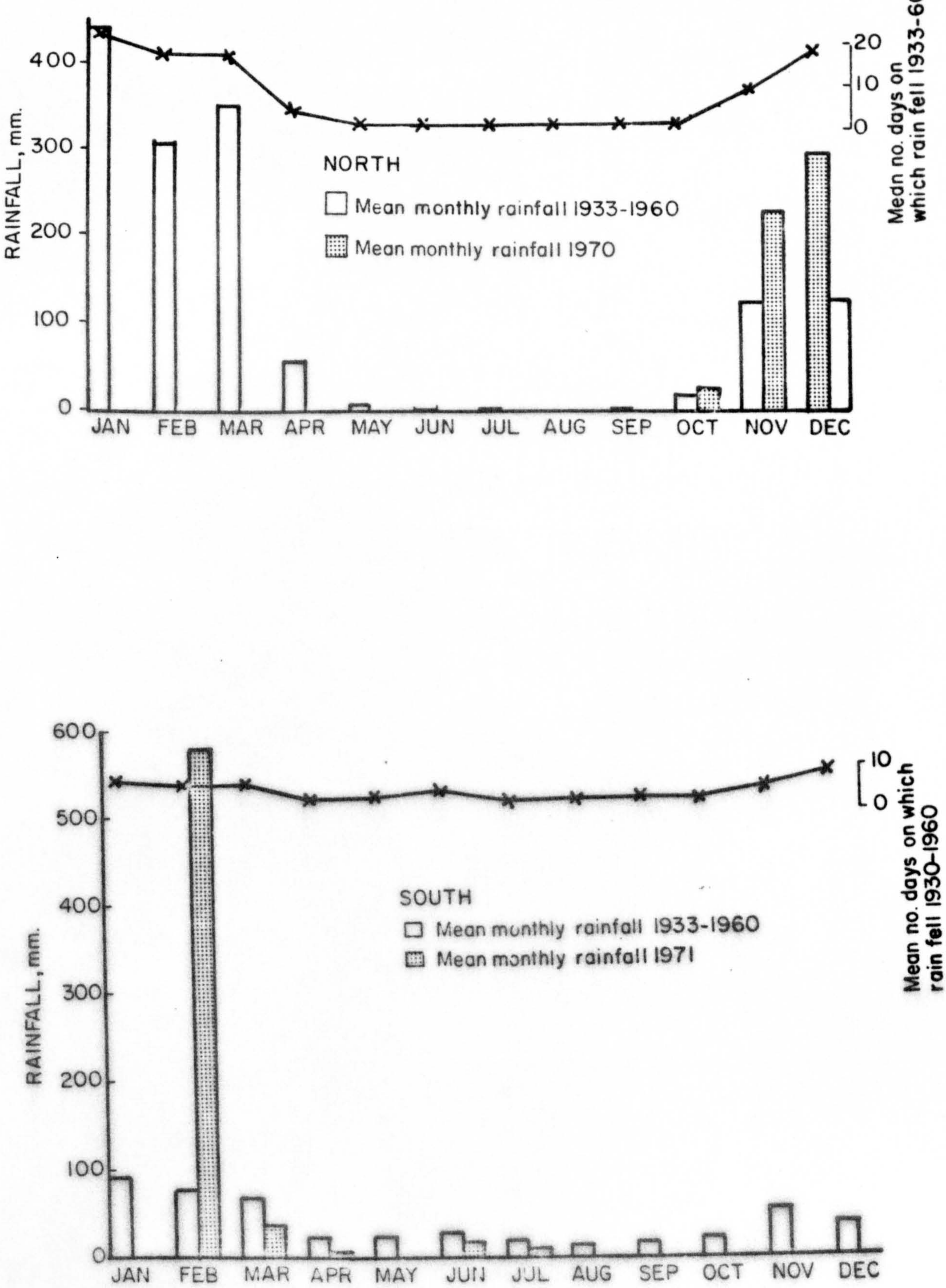
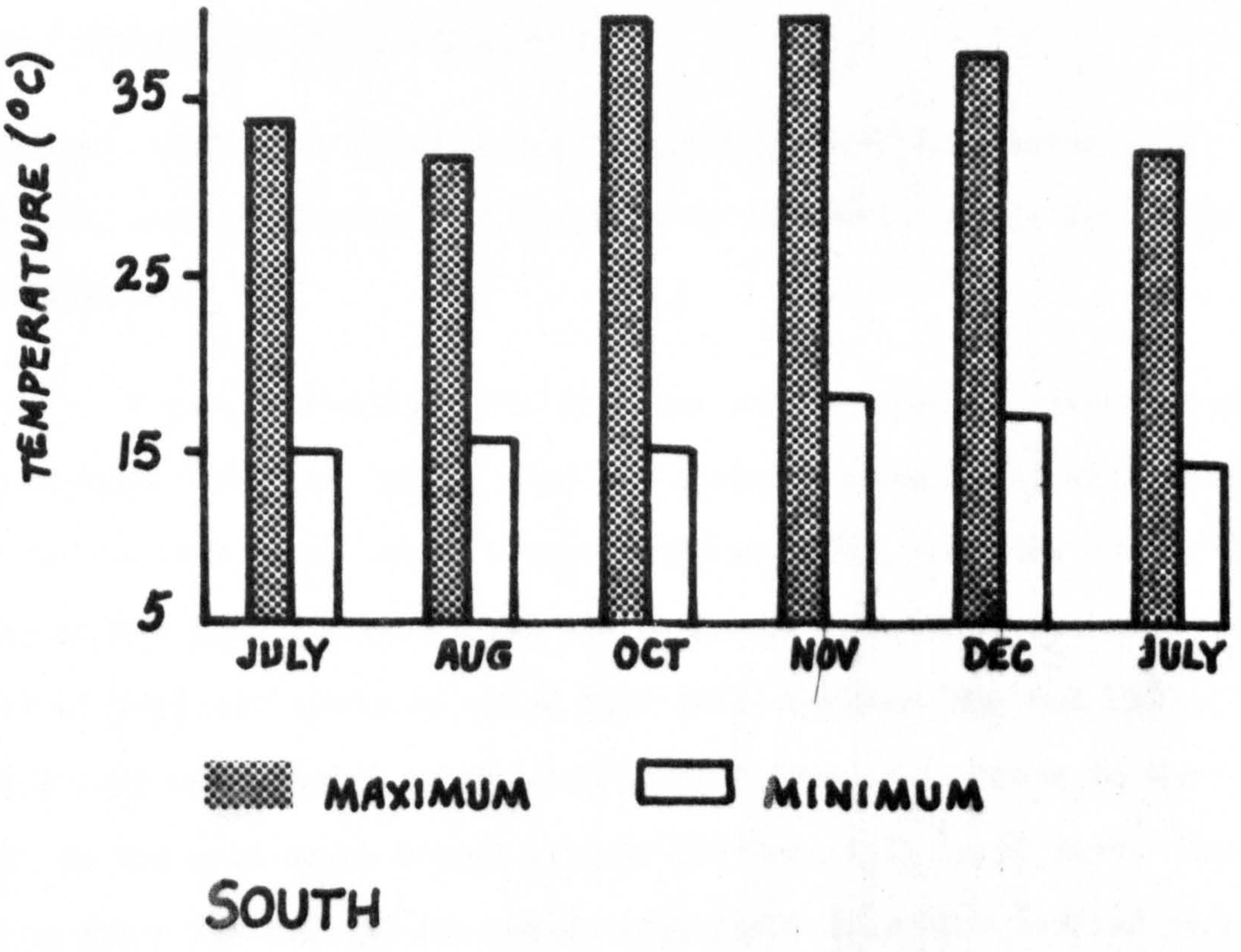
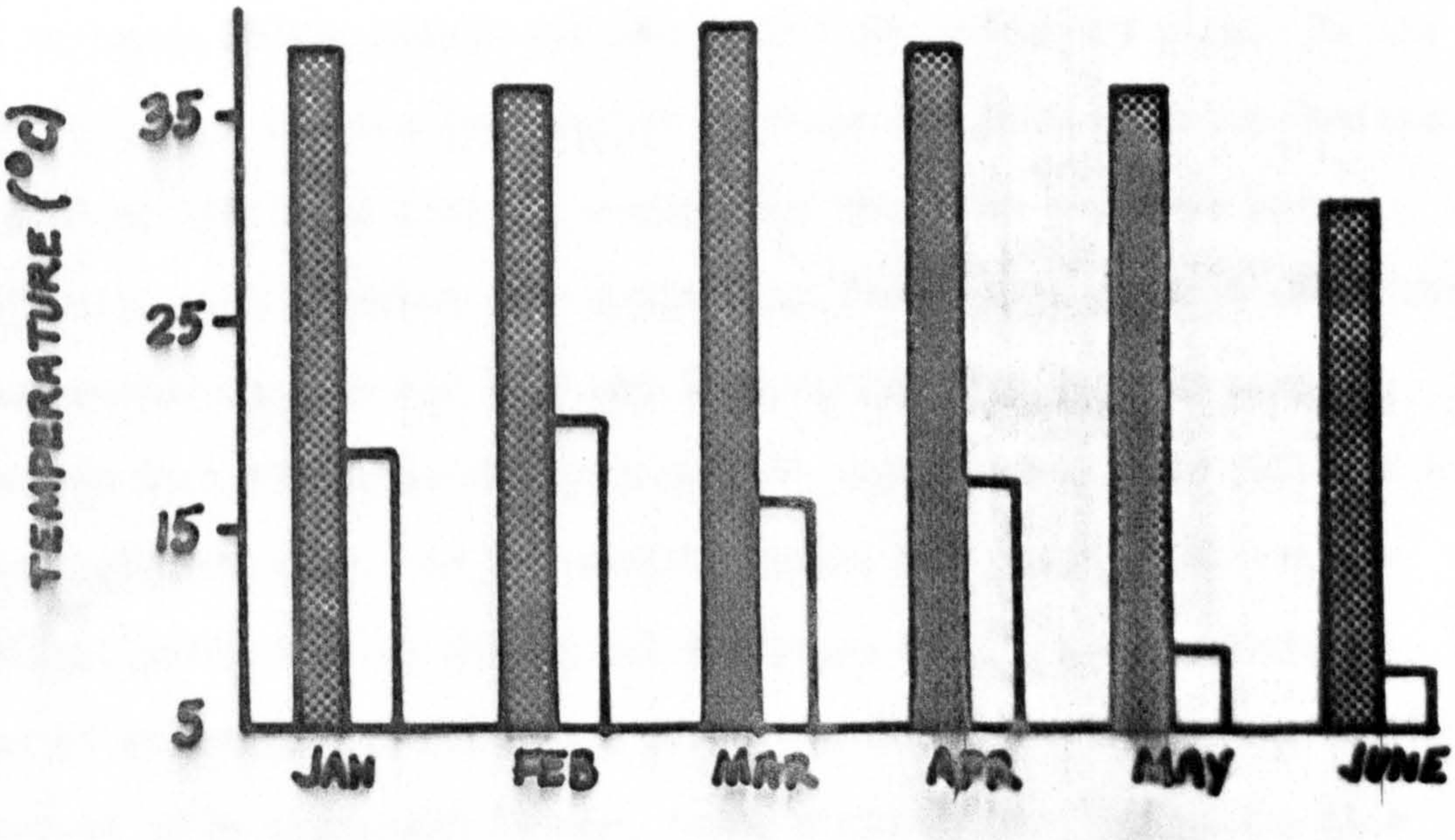

RAINFALL, mm.
400
300
200
100
0
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
NORTH
Mean monthly rainfall 1933-1960
Mean monthly rainfall 1970
20
10
0
Mean no. days on which rain fell 1933-1960
RAINFALL, mm.
600
500
400
300
200
100
0
SOUTH
Mean monthly rainfall 1933-1960
Mean monthly rainfall 1971
10
0
Mean no. days on which rain fell 1930-1960

Fig. 31. Maximum and minimum temperatures recorded in each study area, each month.

NORTH


TEMPERATURE (°C)
35
25
15
5
JULY
AUG
OCT
NOV
DEC
JULY
MAXIMUM
MINIMUM

SOUTH


TEMPERATURE (°C)
35
25
15
5
JAN
FEB
MAR.
APR.
MAY
JUNE

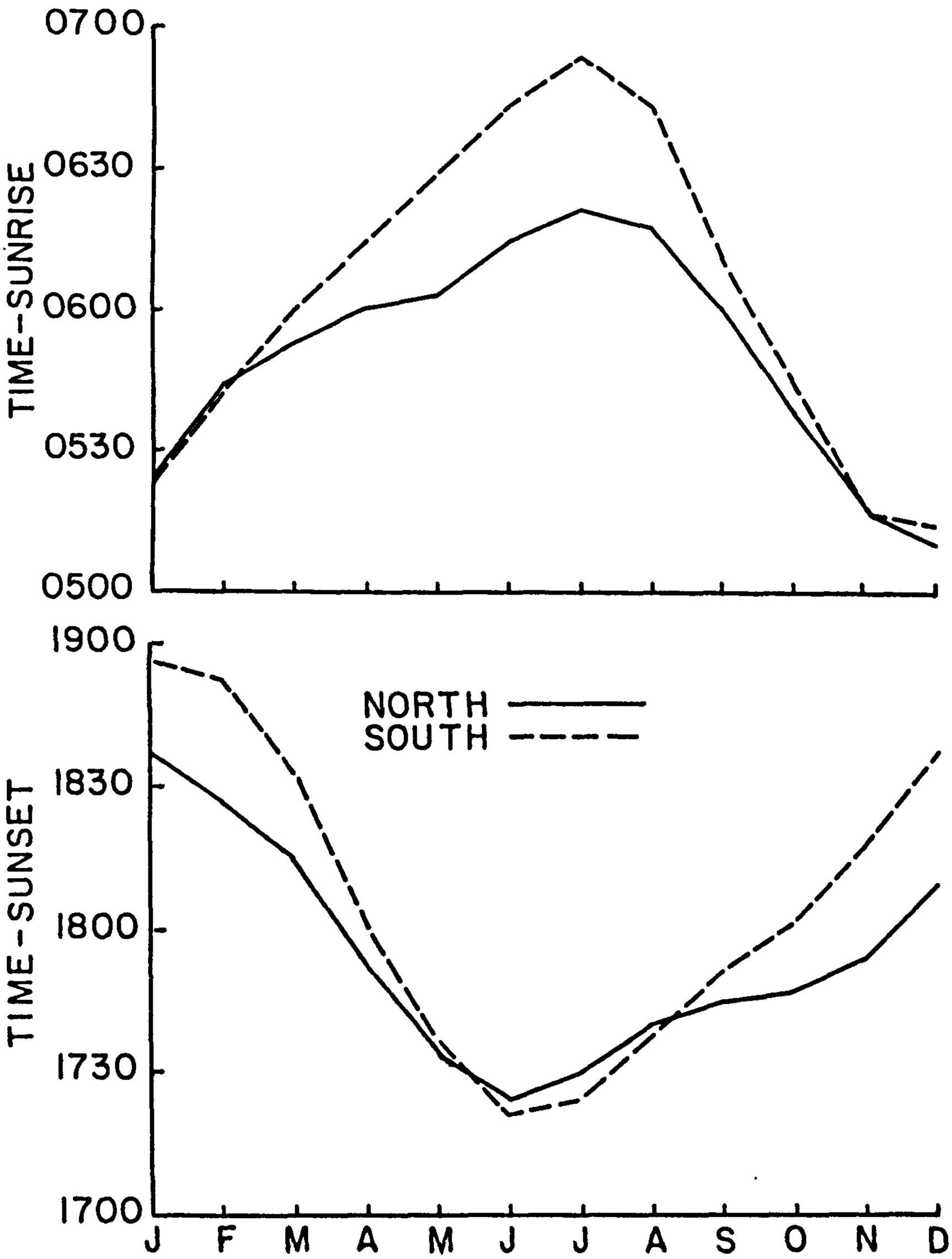
RESULTS

Seasonal variations in climatic factors

Seasonal changes in rainfall and temperature were documented from field data and from information supplied by the Météorologie Nationale de Madagascar.

Rainfall. Figures 29 and 30 show the mean monthly rainfall recorded at meteorological stations 30kms. from the northern study area, and 16kms. from the southern study area, between 1933 and 1960, and also during the months of the field study in 1970 and 1971. It also shows the mean number of days each month on which rain fell, between 1933 and 1960. Where a mean of 1619.2mm. of rain fell in 93 days of the year in the north, in the arid south a mean of only 527.6mm. fell in 62 days. The results shown for 1970 in the north approximate those for earlier years, both in terms of the amount and seasonal distribution of rain. In the south, however, results are similar to those for 1970 (Charles-Dominique and Hladik, 1971) but differ sharply from those for previous years: heavy rain, most of which fell during the three cyclones that swept the region during January and February (the results for January were destroyed when the meteorological station was flooded), was followed by almost total drought. In the earlier years, the general pattern was of slight precipitation throughout the year, with a peak in January. In terms of studying the effects of greatly different environments on the behaviour of P. verreauxi it was, thus, fortunate to be working at a time when differences were at a maximum.

Temperature. Figure 31 shows the maximum and minimum temperatures recorded on a thermometer hung in the shade within the home-ranges of the study groups in each area. Readings were taken every twenty four


0700
0630
0600
0530
0500
TIME-SUNRISE
1900
1830
1800
1730
1700
TIME-SUNSET
NORTH
SOUTH
J F M A M J J A S O N D
MONTH

hours. There was little difference between the maximum temperatures in each area, or between the minimum temperatures during the wet season. However, during the dry season in the south, minimum temperatures fell to a lower level than in the north. Thus, the southern groups were exposed to wider fluctuations in daily temperature during the dry season.

Daylight hours. Figure 32 shows the changes in the time of sunrise and sunset in each area during a full year. In both study areas, there was an approximately three-hour increase in the number of daylight hours during the wet season.

Resting

An inactive animal was said to be resting. This resting category included both "sunning" behaviour and "true" resting but no objective criteria were found to discriminate consistently between them. Thus an inactive animal was always recorded simply as resting, and a separate record was kept of whether it was in the sun or the shade (P. 40). Distinctions were, however, possible at a general descriptive level.

During "true" rest periods animals, singly or in groups of two or more, sat or sprawled, usually in the shade. During the hot wet season in both study areas, animals often moved down to a height of 2-3m. from the ground to rest, and on 19 occasions in the north, and 11 in the south, animals rested sitting on the ground. In the cooler dry season, groups seemed to prefer wide horizontal branches or, in the south, the fork of an Alluaudia tree; associated with this apparent choice of substrate animals were usually at least 4m. from the ground, wide horizontal branches not often occurring below this height. As in the dry season, animals usually sat in the shade during rest periods. Periodic self- and allo-grooming and, in the wet season, play bouts took place during

these rest periods.

"Sunning" behaviour, described by Jolly (1966), occurred after sunrise in the dry season in both study areas before any major activity took place, and sometimes again before the animals settled for the night. On most mornings in the dry season, animals moved on to the first main branches to be struck by the sun and stayed there for about one hour (see Plate VI). Posture varied during these "sunning" bouts from the habitual sitting position, with any part of the animal turned to the sun, to a position in which the animal sat with arms and legs splayed, its head on one side, and its black-skinned ventral surface, only sparsely covered with fur, facing the sun (see Plate XIV). Such behaviour was less frequent in the wet season. Similar accounts of "sunning" have been given for Lemur catta and Lemur fulvus rufus (Jolly, 1966; Sussman, in press).

Locomotion

Adaptiveness of P. verreauxi's locomotor pattern. Napier and Walker (1967) allocated P. verreauxi to the locomotor category of "vertical clinging and leaping" (VCL), defined in terms of a complex of anatomical adaptations. The title of this category aptly describes P. verreauxi's saltatory movement from vertical trunk to vertical trunk when moving through the forest from one food source to another or when fleeing (Plate XIV).

Napier and Walker (1967) discussed the possible adaptive value of this mode of locomotion. They noted Petter's (1962b) comment that "...the leaping type of locomotion is well fitted to predator avoidance..." adding that since there are no large arboreal predators in Madagascar today, the behaviour must be a left-over from late Eocene times when "...predator avoidance must have been highly necessary..." However, it

is possible that predators still contribute significantly to infant mortality (see P. 67). If so, P. verreauxi's mode of locomotion may still have adaptive value for predator avoidance, although there is no evidence to indicate that a springing quadrupedal form of locomotion would be less adaptive.

The authors also postulated that the behaviour permits "...the use of certain restricted habitats where only vertical supports are found, such as the Alluaudia scrub of S.W. Madagascar...." If VCL is a specialization for such habitats, it is difficult to explain the abundance of P. verreauxi and other species with a similar locomotor pattern in deciduous forests throughout the island. Further, although the structure of Alluaudia species contains a larger vertical component than that of other trees, it is an exaggeration to suggest that only vertical supports are available. It is probable that a springing, branch-running quadruped would be equally well adapted in this habitat.

Finally, Napier and Walker (1967) commented "...The limitations imposed by the vertical clinging and leaping habit upon feeding behaviour are also quite marked; the large forms, especially, are at a disadvantage when feeding in small branch milieu..." However, the limited locomotor analysis (P.223) and other observations made in the course of this field study suggest that P. verreauxi's mode of locomotion is adaptive in allowing it to reach food located at almost any part of a tree. This is endorsed by Jolly (1966) who commented that P. verreauxi feeding among terminal branches display more varied and flexible postures than Lemur catta. It seems unlikely that P. verreauxi is ecologically separated from the quadrupedal lemurs by reduced versatility in locomotion.

Sussman (in press) describes the locomotion of Lemur fulvus rufus and Lemur catta in the trees: "When groups of L. f. rufus moved horizontally through the trees, the animals ran along the fine end

Fig. 33. Distribution of time spent in different substrate categories by the northern and southern study groups.

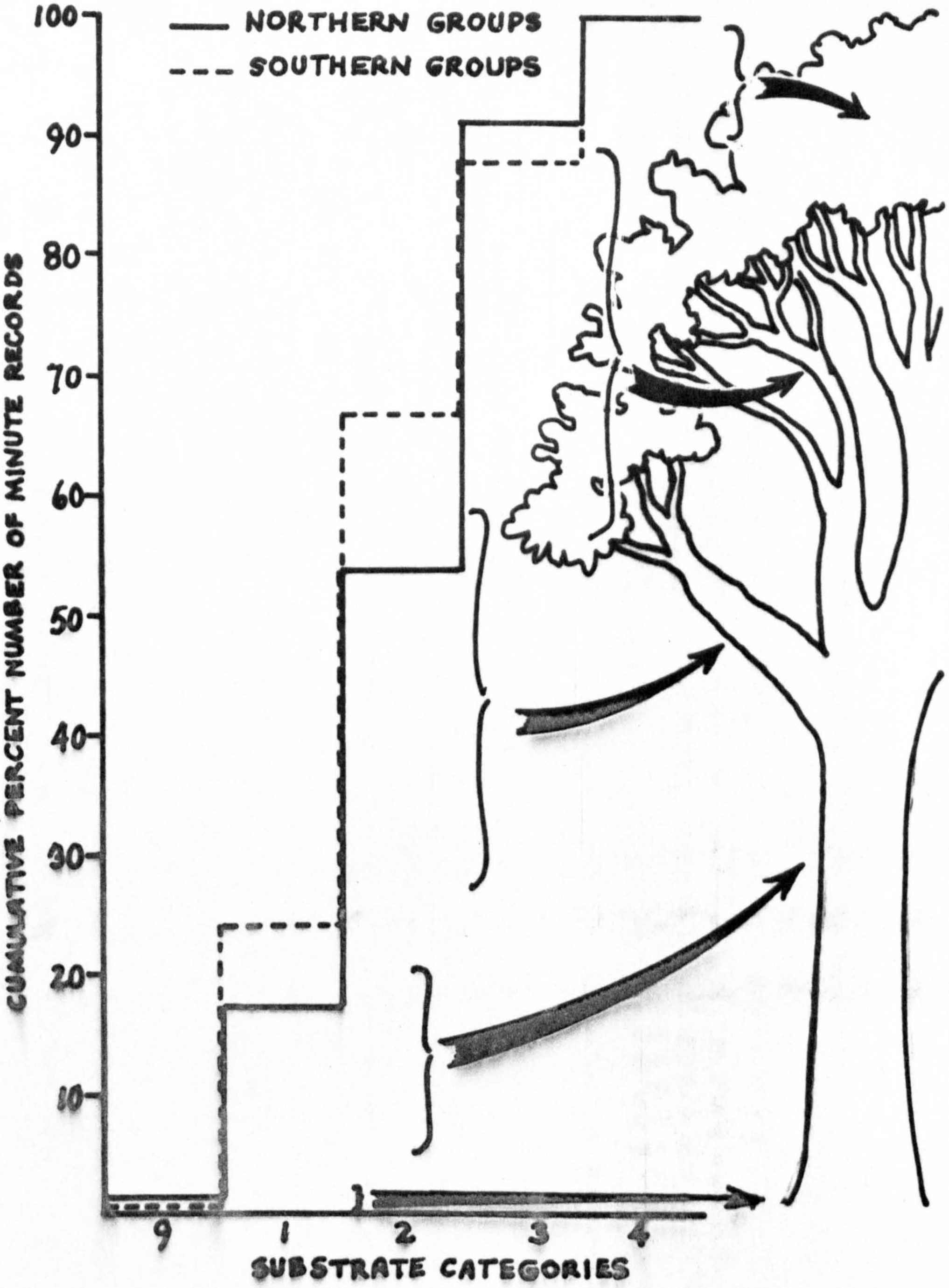
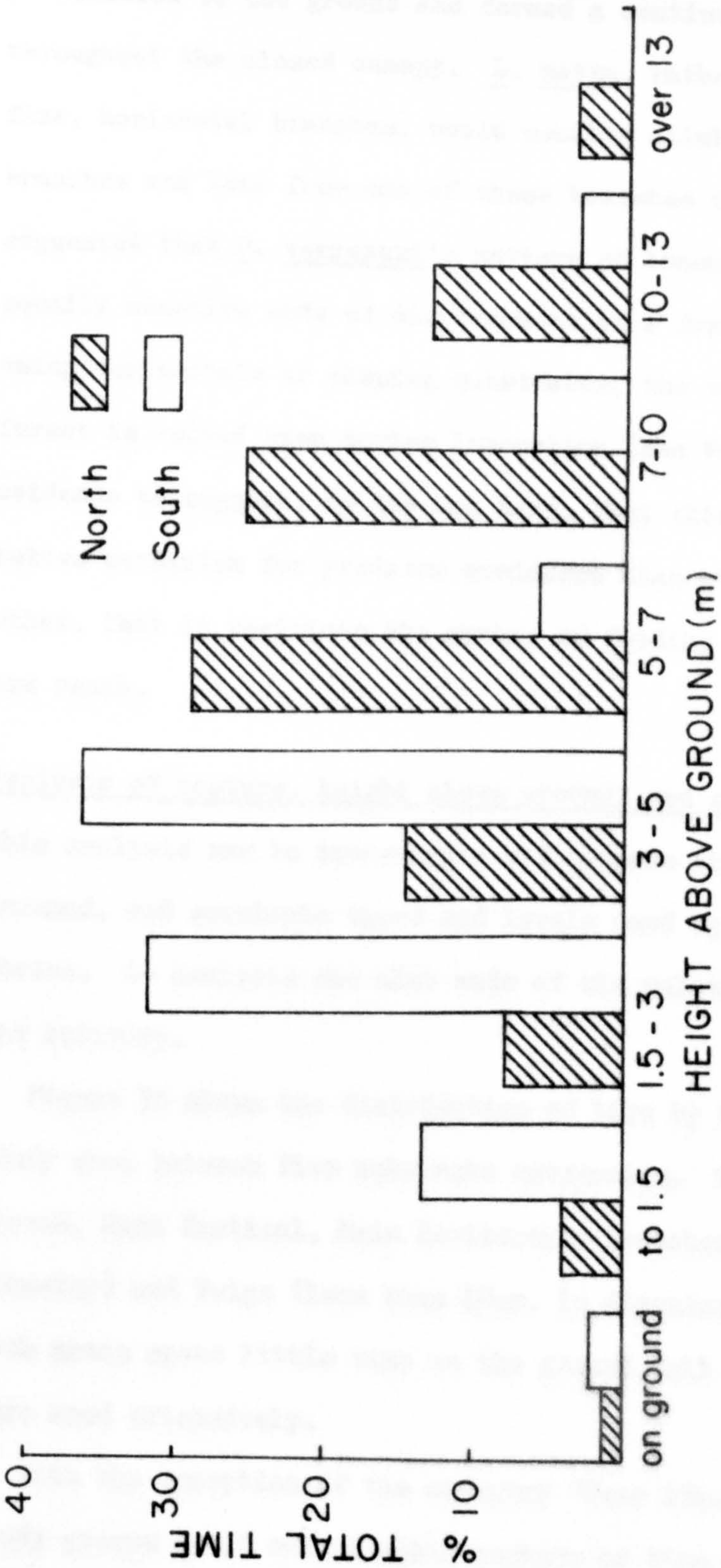

NORTHERN GROUPS
SOUTHERN GROUPS
CUMULATIVE PERCENT NUMBER OF MINUTE RECORDS
100
90
80
70
60
50
40
30
20
10
9
1
2
3
4
SUBSTRATE CATEGORIES

Fig. 34. Time spent at different heights above ground by the groups in each study area.


North
South
over 13
10-13
7-10
5-7
3-5
1.5-3
to 1.5
on ground
HEIGHT ABOVE GROUND (m)
40
30
20
10
% TOTAL TIME

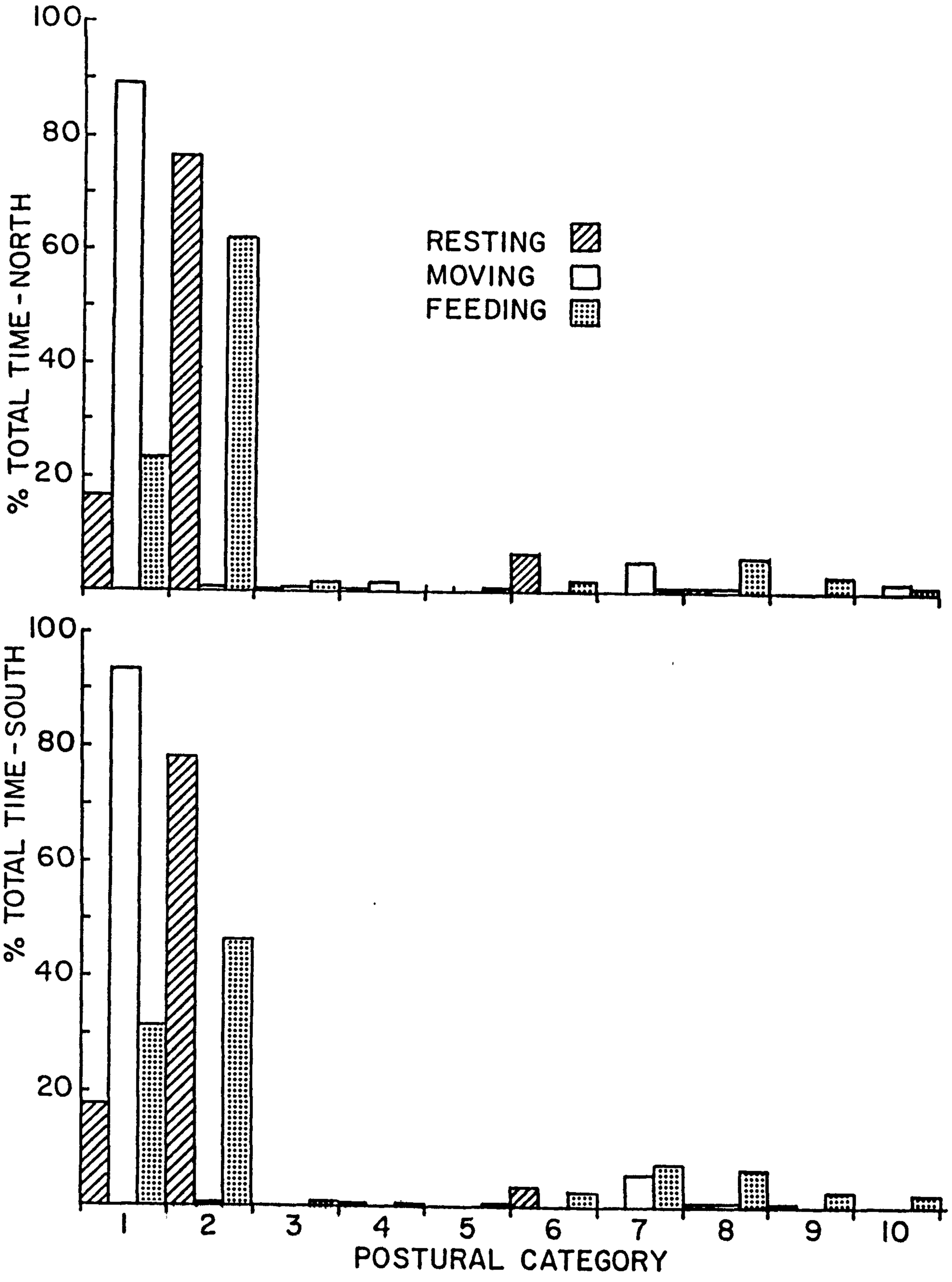
branches of the large trees. These branches were generally horizontal in relation to the ground and formed a continuous series of pathways throughout the closed canopy. L. catta, rather than moving along the fine, horizontal branches, would usually climb the large, oblique branches and leap from one of these branches to another..." It is suggested that P. verreauxi's pattern of locomotion is simply a third, equally adaptive mode of displacement in a forest habitat. Instead of using horizontals or sloping substrates, the vertical component of the forest is relied upon during locomotion (see Figure 33). There is no evidence to suggest, on the one hand, that this locomotor pattern is a better mechanism for predator avoidance than other patterns or, on the other, that it restricts the number of feeding stations which P. verreauxi can reach.

Analysis of posture, height above ground, and substrate use. The aim of this analysis was to investigate and compare the range of postures assumed, and substrate types and levels used by the study groups in each forest. An analysis was also made of the relationship between posture and activity.

Figure 33 shows the distribution of time by the two groups in each study area between five substrate categories. These categories were Ground, Main Vertical, Main Horizontal, Branches (less than 6cm. in diameter) and Twigs (less than 1½cm. in diameter). Although animals in both areas spent little time on the ground, all other substrate categories were used extensively.

With the exception of the category "Over 13m." in the south, the study groups spent considerable amounts of time at all levels in each forest (see Figure 34). These levels represented only height above the ground: in neither study area was the vertical composition of the forest sufficiently uniform to correlate each level with a character-

Fig. 35. Time spent in different postures while resting, feeding and moving, by the four study groups.


100
80
60
40
20
% TOTAL TIME-NORTH
RESTING
MOVING
FEEDING
100
80
60
40
20
% TOTAL TIME-SOUTH
1
2
3
4
5
6
7
8
9
10
POSTURAL CATEGORY

istic structure (c.f. Sussman, in press). The southern groups tended to spend more time at lower levels than the northern groups. Factors contributing to this difference were the overall lower stature of the southern forest (see Figure 6), and the fact that most of the taller trees in the south were Alluaudia ascendens and Alluaudia procera; the extremities of the thin, spiny vertical branches of these species provided no regular or firm support for locomotion and were a source of food only in September. Animals were rarely seen high on these branches at any other time.

Figure 35 shows the amount of time spent in different postures while resting, feeding and moving, by the four study groups. As with the analysis of substrate types, there was a striking similarity in the results for each study area: when moving, the posture of animals in both areas was almost exclusively upright. Animals generally sat when resting. In both study areas, over 75% of feeding was done in a sitting or VCL position. However, it was in this activity that the greatest diversity of posture was shown. This diversity probably enabled animals to reach food located on the periphery of trees in the fine branch niche.

The results described above indicate the ability of P. verreauxi to move regularly in different parts of trees, at different heights, using a variety of postures. However, the full significance of the results, and of the differences and/or similarities between the two study areas, could be fully interpreted only if a complete analysis were made of the differential availability of different substrate types in each forest. From such an analysis it could be inferred to what extent animals selected their substrate rather than simply used what was most readily available. The similarity of the results for posture and substrate use in each study area contrasts with the considerable differences apparent between the physical structure of the two forests. Thus, it is probable

Fig. 36. Mean number of minute records per hour on which subjects were recorded feeding throughout the day, showing seasonal changes.

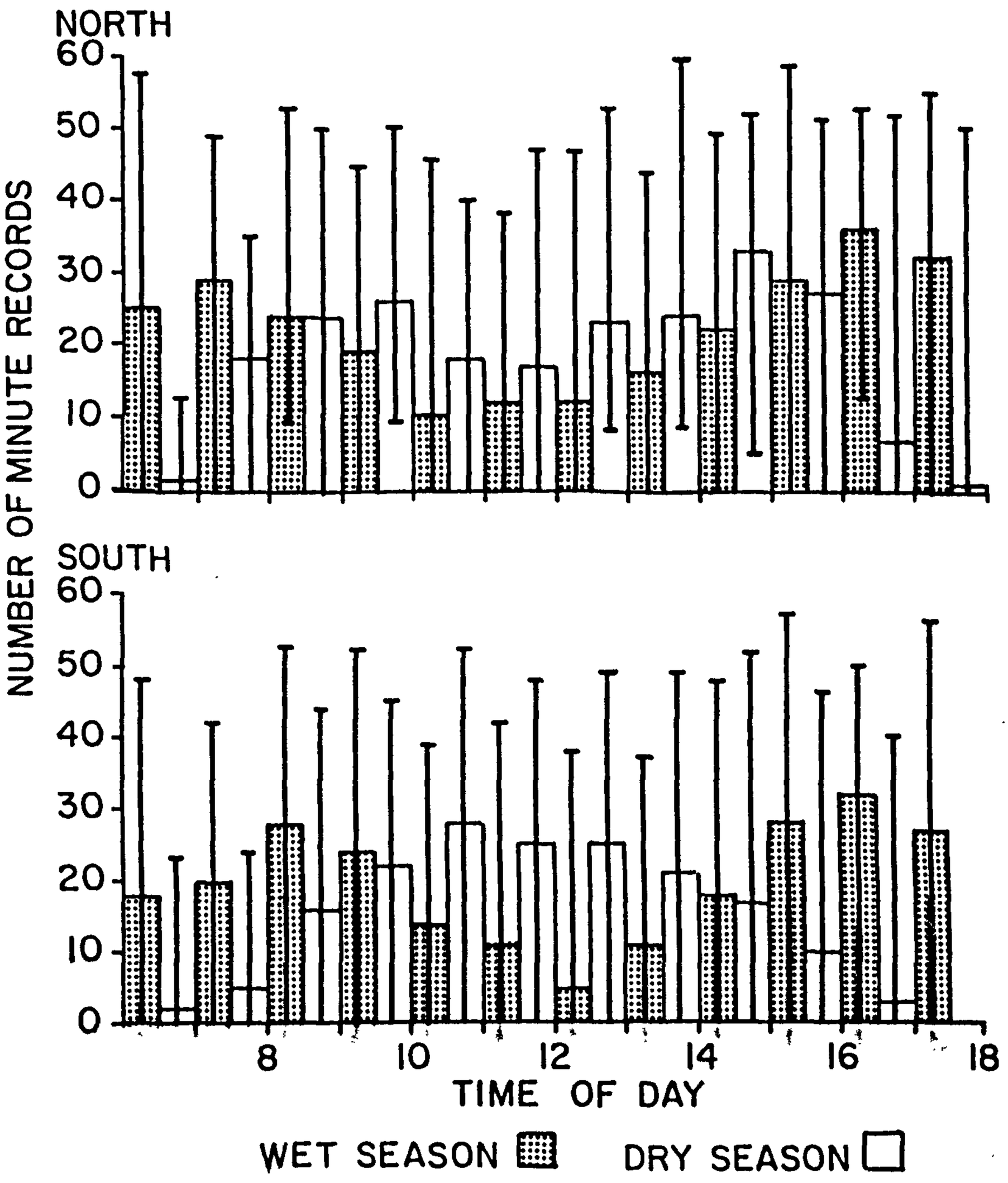
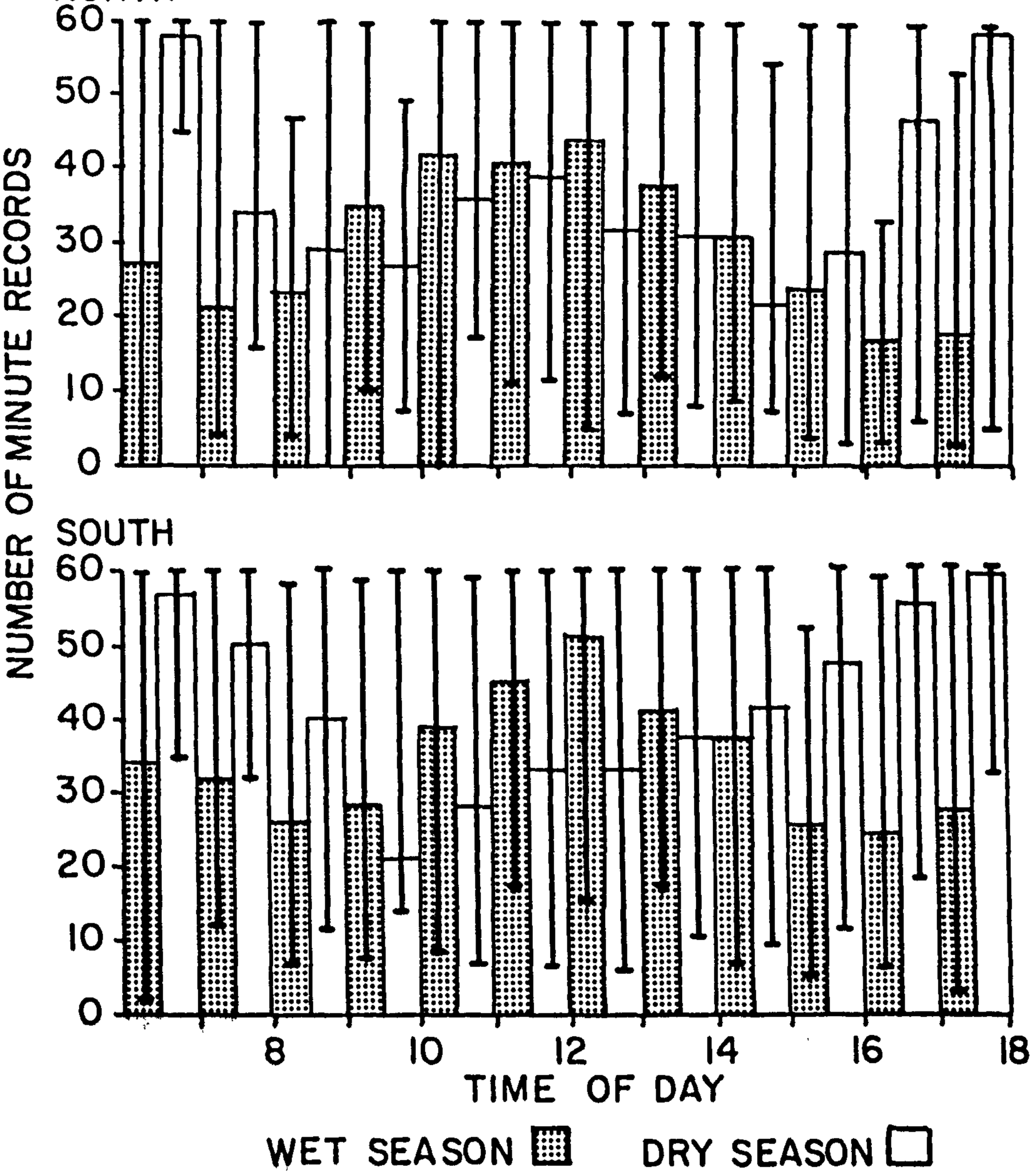

NORTH
60
50
40
30
20
10
0
SOUTH
60
50
40
30
20
10
0
NUMBER OF MINUTE RECORDS
8
10
12
14
16
18
TIME OF DAY
WET SEASON
DRY SEASON

Fig. 37. Mean number of minute records per hour on which subjects were recorded resting throughout the day, showing seasonal changes.


NORTH
60
50
40
30
20
10
0
NUMBER OF MINUTE RECORDS
SOUTH
60
50
40
30
20
10
0
8
10
12
14
16
18
TIME OF DAY
WET SEASON
DRY SEASON

that animals were highly selective in their choice of substrate, and that similarities in posture were related to this.

On 13 occasions an animal was seen to progress hanging by its arms alone and moving one hand over the other three or four times. Hanging by the arms without progression was commonly seen after a rest period, and seemed to be a form of "stretching" by the animal. During play bouts participants might hang by arms or legs alone, wrestling with and attempting to dislodge each other. Twice, animals on the ground moved one or two metres with waddling steps, instead of the habitual bipedal hop. Only once was an animal seen to move quadrupedally on the ground (see Section VIII).

The initial clumsiness of infants' efforts to move about unaided disappeared in the course of their development (in prep.) and adult P. verreauxi were agile and rarely missed their footing. On only five occasions outside the mating season were animals seen to fall, and three of these times the animal involved was a juvenile. One collision between animals in mid-air was seen.

Seasonal variations in daily activity patterns

Recording techniques were discussed in detail in Part I. Figures 36 and 37 show the mean number of minute records per hour on which subjects were recorded feeding and resting, respectively, throughout the day; the range of variation is also shown. The daily data for each area were grouped into wet and dry season means, which are plotted separately in Figures 36 and 37.

For each season in each area, results are based on observations collected from 0600h. - 1800h. on 18 days, evenly distributed through three months. Observations were approximately evenly distributed between

ten animals belonging to two groups in the south, and between eleven animals belonging to two groups in the north. A Kruskal Wallis One-Way Analysis of Variance Test was used to evaluate the significance of differences between observations on the various age/sex classes, and data were combined only where differences were not significant. Statistical comparison of the mean amount of time spent in a given activity at different times of day or in different seasons was not possible because the data were frequently not independent, consisting of repeated observations on the same animal. However, in view of the gross nature of the difference between seasons in each area, statistical tests of significance are probably superfluous.

Feeding. In both areas, the pattern of feeding in each season, and the nature of the change between seasons were similar: during the wet season, feeding began early, reaching a peak between 0700h. and 0900h. This was followed by a gradual decrease until midday, by which time very little feeding was taking place. Between 1300h. and 1400h. the amount of time animals spent feeding began to increase once more, reaching a peak in the late afternoon. In the wet season, animals in the north spent a mean of 37% of total time each day feeding, and in the south a mean of 32.8%.

During the dry season, intensive feeding began later and ended earlier in both study areas; however, in the north there was still a falling-off in feeding rates at midday, although it was less marked than in the wet season. By contrast, feeding rates in the south slowly built up throughout the morning to reach a peak at midday and then decreased in the afternoon at almost the same speed, so that the Figure 36 dry season results show a nearly symmetrical curve. Considering overall percentages, the southern groups spent a mean of 24.2% of total time each day feeding in the dry season, and northern groups a mean of 30.3%.

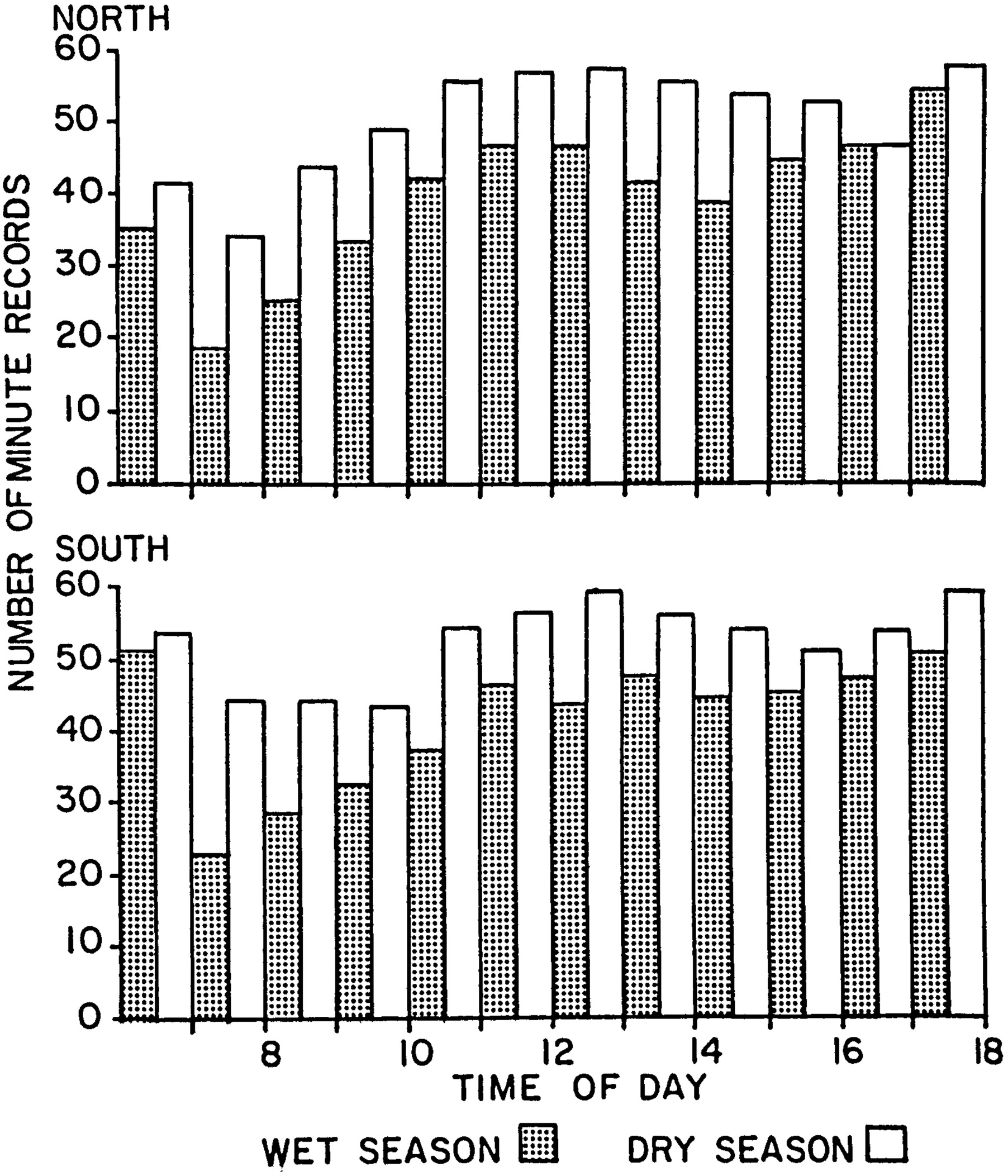
Resting. Since animals in both areas spent most of their time either resting or feeding, patterns of resting inevitably dovetail neatly with those of feeding. In the dry season in both areas, early morning resting peaks were followed by a decline in time spent resting. In the south this reached its lowest point between 0900h. and 1000h., after which there was a continuous build-up until by 1700h. almost 100% of total time was spent resting. The northern groups deviated from this resting pattern as they did from the southern groups' feeding pattern: the slight, midday decrease in feeding in the dry season was associated with a slight, midday increase in resting. The northern groups spent a mean 61.5% of total time each day resting in the dry season, and the southern groups a mean of 69.5%.

In the wet season, early morning counts of time spent resting were relatively low in both areas, and then built up to a midday resting peak; as the afternoon feeding bout began, time spent resting once more decreased. The northern groups spent a mean 50% of total time each day resting in the wet season, and the southern groups a mean 56.8%.

Range of variation. The range of variation in the amount of time spent feeding/resting in any given hour was very wide. However, though animals frequently rested without interruption for a whole hour at a time, they were never observed to feed without interruption for so long a period. The converse necessarily applied: although records for most hours were gathered, particularly in the south, in which there was no feeding noted, animals always spent some part of every hour resting.

The range of variation in activity patterns was such that an animal's activity at a given hour could never be predicted with certainty. Although the actual sequence and duration of activities seemed to remain fairly constant, the absolute time of day at which an activity took

Fig. 38. Amount of time during the day spent in the shade by animals in each study area, in each season.


NORTH
60
50
40
30
20
10
0
SOUTH
60
50
40
30
20
10
0
NUMBER OF MINUTE RECORDS
8
10
12
14
16
18
TIME OF DAY
WET SEASON
DRY SEASON

place apparently depended largely upon the time at which the whole sequence of activities for the day began.

Seasonal variations in exposure to sunshine

Figure 38 shows the amount of time during the day spent in the shade by animals in each study area. There was little difference between the amount of time spent in the shade by animals in each study area during the wet season or during the dry season. However, in both areas much more time was spent in the shade during the wet season than during the cooler dry season.

Although during the first hour of recording, around sunrise, a considerable proportion of time was spent in the shade, the amount spent in the shade between 0700h. and 0800h., in both seasons, was the least of all hours. From 0800h., the amount of time spent in the shade per hour increased fairly consistently until mid-afternoon when, in both seasons and in both areas, there was a slight decrease in the amount of time spent in the shade. By 1800h., however, the counts again reached the midday peak of almost 100% of total time being spent in the shade, and both these peaks exceeded that found in the first hour of observations.

DISCUSSION AND CONCLUSIONS

The significance of activity patterns

It is well known that gross differences exist in the bout length and patterns of activity between primate species as well as between whole Orders of the Mammalia. These differences are often associated with broad differences in diet. The fruit and insect-eating capuchin monkey, Cebus capuchinus, for example, spends a large proportion of daylight

hours foraging (Hladik and Hladik, 1969), compared with 10% for leaf-eating howler monkeys, Alouatta villosa, living in the same forest (Richard, 1970). In Africa, savannah-living, omnivorous baboons spend most of the day foraging (Altmann and Altmann, 1970; Stoltz and Saayman, 1970), while the leaf, shoot and fruit-eating red colobus monkey, Colobus badius, spends only 25-30% of its day feeding (Clutton-Brock, in press).

Variation of a similar nature is also found at higher taxonomic levels. Diurnal mammalian insectivores and carnivores usually spend more time foraging and less resting than herbivores: the frugivorous/insectivorous coati, Nasua narica, spends most of the day foraging with only occasional rest periods (Kaufmann, 1962). Neal (1970) reports that packs of the banded mongoose, Mungos mungo, "...covered large distances, foraging as they went..." each day. In contrast, ungulates feed for periods each day comparable to those of the largely leaf-eating primates: the male Uganda cob spends 31-43% of its time feeding, depending on its social status (Leuthold, 1966). The warthog, a browser, spends 20-40% of its time feeding, depending on its body size (Clough et al., 1970).

These variations in time spent feeding may be influenced by a number of factors. These include the availability, distribution and density of food sources as well as differences in the food's nutritional value and the animal species' efficiency in assimilating it.

The daily timing of activities varies from the steady, day-long foraging, interspersed with short rest periods, of omnivorous or insect-eating primate species (Hladik and Hladik, 1969; Altmann and Altmann, 1970) to the two feeding peaks, one in the early morning and one in the late afternoon, of many vegetarian species (Van Lawick Goodall, 1968; Hall and Gartlan, 1965; Sussman, in press). Clutton-

Brock (in press) also found a midday peak in feeding in red colobus comparable to that reported for howler monkeys (Chivers, 1971) and the mangabey (Chalmers, 1968).

Since abrupt seasonal changes in the current study, particularly in the south, were associated with extensive changes in the daily activity pattern of P. verreauxi, this provided a good opportunity to attempt to identify some of the parameters influencing the pattern of performance of daily activities. Changes in these parameters may be partially responsible for inter-specific as well as intra-specific variations in activity patterns.

Seasonal changes in activity patterns

The quantitative and descriptive results presented in this Section show that in both areas there was a consistent daily pattern of activities, and that this pattern changed radically between seasons. The factors determing the timing of activities from day to day, and the seasonal changes in activity patterns are complex and thus difficult to identify. They can be loosely categorized as internal and external. Internal factors include physiological processes such as energy production, food digestion and secretion of hormones. External factors include climate and food availability. This distinction is not clear, in that internal physiological processes must be adapted to external factors if the species is to survive, but for this discussion they are considered separately.

a) Internal factors. The extensive daily variation in time spent in a given activity at any given time of day has already been noted. Total time spent each day in any given activity remained constant, however. Further, the sequence and bout-length of activities appeared to remain

approximately constant within each season. It therefore seems likely that on a daily basis, internal mechanisms are important in regulating an animal's sequence of activities and the amount of time spent in each: the sequence remains constant in order and in bout-length of activity, regulated by physiological requirements, but the time of day at which the sequence is initiated may vary, thereby causing the great ranges shown in Figures 36 and 37. For example, after a period of high energy expenditure, a period of inactivity may be necessary to dissipate an excess heat load. Similarly, after a feeding bout, the digestive process may require a period of rest.

Internal factors should also be considered with respect to gross seasonal changes: it is possible, for example, that activity patterns in the wet season may be influenced by hormonal changes relating to the mating season, which occurs towards the end of that season.

Despite the great variability in activity within each period of the day, an overall pattern of activity in each season did appear to be related to the time of day. For this reason, external factors must be sought in addition to internal regulating mechanisms.

b) External factors. The influence of food distribution and availability was discussed in Section IV.

In both areas day length varied between seasons by about three hours. Pariente (in press) has found that light levels provide critical threshholds of activity for Lepilemur mustelinus; he found that individuals of this species were inactive in the wild until the light level decreased to a certain value. Similarly, in the early morning activity ceased abruptly when the light present in the forest reached a critical level. It could be argued, thus, that the increased activity (see also Section V) and changes in activity pattern seen in P. verreauxi in the wet season were related to an increase in day length. However, animals

were usually moving and feeding in the halflight before sunrise in the wet season, and continued to feed in the evening until it was too dark for observations to be made. This contrasts with behaviour in the dry season, when animals rarely moved until two or three hours after sunrise, and were usually settled for the night about three hours before sunset. Thus light levels did not play a crucial role in determining the onset and cessation of activity in the groups studied, although it may have been a minor contributing factor.

Ambient temperature and, closely associated with this, solar radiation may be important climatic factors determining daily and seasonal changes in activity patterns. Figure 38 showed that more time was spent in the sun in the dry season than in the wet, and that more time was spent in the sun in the early morning than later in the day in both seasons, in both study areas. Two factors contributing to the seasonal differences are:

1) reduced availability of shade, due to the decrease in tree foliage in both areas in the dry season, and
2) the decreased number of hours of sunshine each day, due to the more overcast sky of the wet season. Countering this, however, the greater length of days in the wet season would tend to increase the number of hours of possible sunshine each day.

It is also possible that changes in the behaviour of the animals may have contributed to seasonal differences. It could be argued that because of the lower night-time temperatures of the dry season, animals sought the sunshine, particularly in the early morning, in order to raise their body temperatures. Seasonal differences in feeding behaviour may have affected the position of animals in the trees and, for

example, in the dry season they fed more on terminal twigs which were more likely to be in the sun than areas nearer the centre of trees. Differences in exposure to sunlight between early morning and later periods of the day could similarly be explained in terms of a difference in the location of feeding or locomotor activities at these times, the difference in exposure to sunshine being purely incidental. However, there is no evidence that the location of animals' feeding or locomotor activities did change consistently in such a way either seasonally or during the day. It is more plausible that the animals did seek or avoid the sunshine according to the level of ambient temperatures. This, coupled with observations of behaviour such as adopting characteristic "sunning" postures or huddling postures, leads me to believe that certain behavioural adaptations related to thermo-regulation were present.

Rainey (1970) demonstrated behavioural adaptations in the rock hyrax, Heterohyrax brucei, without which it was unable to maintain its body temperature. These adaptations included:

1) huddling at night, which reduced the total heat loss of the two animals involved by 30%;
2) increased amount of body contact maintained with the rock surfaces, depending on ambient and internal temperature; and
3) "sunning" behaviour in the early morning, through which an animal could raise its temperature by $4^{\circ}C.$ in one hour.

The thermo-regulatory value of these behavioural patterns was determined by subjecting animals in the laboratory to comparable ambient temperatures while not permitting the behaviour associated with them in the wild. This result is corroborated by Bourliere et al.'s (1953, 1956) investigation of the relation of rectal temperature of various prosimian species in captivity to ambient temperature fluctuations. Under these conditions animals, and particularly members of the smaller species,

were unable to maintain their body temperature. However, P. verreauxi was not among the species studied. Until similarly controlled experiments can be carried out on this species, it can only be broadly stated that the animals studied slept in huddles, particularly in the cooler, dry season, spent much of their time in the sun in the early morning, and in the dry season adopted characteristic sunning postures. It is probable that "sunning" behaviour occurred mainly in the dry season because it was at this time that night-time temperatures were at a minimum. In the wet season, when mean temperatures were higher, a prolonged rest was taken in the shade at midday when temperatures were at a maximum.

Whether daily and seasonal differences in exposure to sunshine were a result of adaptive behaviour or environmental changes or were simply incidental, the fact of these differences remains. Schmidt-Nielson (1965) has discussed the problems involved in the measurement of thermo-regulatory parameters, and stressed repeatedly the difficulties and hence the lack of data on this subject. He stated that "The difficulties in describing the heat exchange between the organism and the environment are so formidable that not even for man under constant conditions in the laboratory when air and radiation temperatures are kept at the same constant level has it been possible to describe adequately the complete heat exchange..." From the present study it can only be said that in the dry season, particularly in the south, P. verreauxi was subject to very low minimum temperatures at night and to very high maximum temperatures during the day. It seems probable that animals helped to regulate their body temperature during the hot wet season and the hottest part of the day in both seasons by reducing the amount of time spent in the sun during that period. Other behavioural changes were associated

with low temperatures. Further investigation of this aspect of P. verreauxi's relationship to its environment is necessary.

SUMMARY

1) Activities were recorded in nine categories, but in the discussion of daily activity patterns, only resting and feeding/foraging are considered: almost all movement took place at the beginning, during and at the end of feeding bouts and were associated with foraging behaviour or with movement to a preferred resting tree. The timing of the remaining four, relatively rarely occurring activities is described elsewhere.

2) A mean of 1619.2mm. of rain fell in 93 days of the year in the north, between 1933 and 1960. In the south, rain fell in January and February, with almost total drought during the rest of the year.

3) There was little difference between the maximum temperatures in each area or between the minimum temperatures during the wet season. However, during the dry season in the south, minimum temperatures fell to a lower level than in the north.

4) In both study areas, there was an approximately three hour increase in the number of daylight hours during the wet season.

5) An inactive animal was said to be resting. No operational definition was found to distinguish "sunning" from resting. However, resting occurred at any time, and animals usually sat or sprawled in the shade. In contrast, "sunning" occurred after sunrise in the dry season before any major activity took place: animals sat exposed to the sun and sometimes assumed characteristic sunning postures.

6) P. verreauxi's locomotion has been described as "vertical clinging and leaping." This may be adaptive for predator avoidance, although there is no evidence to indicate that a springing quadrupedal form of

locomotion is less adaptive. It is unlikely to be an adaptation for restricted habitats where only vertical supports are found, because the species is found in deciduous forests throughout the island. Further, it is an exaggeration to suggest that only vertical supports are available in these habitats. It is also unlikely that vertical clinging and leaping imposes restrictions on feeding behaviour. It is suggested that P. verreauxi's pattern of locomotion is equally, but not necessarily more, adaptive than quadrupedalism, and that it should be viewed as an alternative, adaptive mode of displacement.

7) Although animals in both areas spent little time on the ground, all other substrate categories were used extensively. With the exception of the category "over 13m!" in the south, the study groups spent considerable amounts of time at all levels in each forest. The relationship between posture and activity was examined and found to be similar in both areas: the greatest diversity of posture was exhibited when animals were feeding. In toto, these results indicate that P. verreauxi habitually used most parts of trees, most levels of the forest, and a variety of postures. The similarity of the results for posture and substrate use in each study area contrasts with the considerable differences apparent between the physical structure of the two forests. Thus it is probable that animals were highly selective in their choice of substrate, and that similarities in posture were related to this.

8) In both areas, the pattern of feeding in each season and the nature of the change between seasons were similar. Since animals in both areas spent most of their time either resting or feeding, patterns of resting inevitably dovetailed neatly with those of feeding. The range of variation in the amount of time spent feeding/resting in any given hour was very wide, despite the overall existence of "patterns."

9) There was little difference between the amount of time spent in the

shade by animals in each study area during the wet season or during the dry season. However, in both areas much more time was spent in the shade during the wet season than during the cooler dry season.

10) Broad differences in the bout length and pattern of activities are often associated with broad differences in diet. For example, diurnal mammalian insectivores usually spend more time foraging and less resting than herbivores.

11) In both areas there was a consistent daily pattern of activities, and this pattern changed radically between seasons. Factors determining the timing of activities from day to day can be loosely categorized as internal and external. Internal factors include physiological processes such as energy production, food digestion and secretion of hormones. External factors include climate and food availability.

SECTION VII: SOCIAL STRUCTURE

INTRODUCTION

The aim of this Section is to provide a detailed account of intra-group relationships outside the mating season. In Section VIII, the brief mating season and the period immediately preceding it are described, and in the Discussion part of that Section, the mating season is considered as an integral part of a dynamic social system in addition to being simply a period of receptivity and impregnation.

The analysis is based on data collected for Groups II, III and IV on agonistic and friendly behaviour. Only general figures are given for Group I in which not all animals were easily identifiable. For this reason the data on this group are less reliable.

RESULTS

Description of agonistic behaviour

Aggressive behaviour. An animal that displaced, threatened, bit or cuffed another animal in its own group was considered to be the aggressor in an agonistic encounter. Cuffs, given with the hand, and bites, generally administered on the back of the neck or limb extremities, were both usually accompanied by a "cough" or "hack" vocalization. Male A was said to have displaced male B if, as he approached, male B glanced at him rapidly and leapt off at once, or if male B adopted a submissive posture (see below) and subsequently leapt off. Staring, or lunging in the direction of an animal were considered as threats. They resulted in the threatening animal displacing the recipient of the threat, or in the recipient adopting a submissive posture.

TABLE 17: Frequency of agonistic encounters and situations in which they were observed.

Group	Total Number of Agonistic Encounters	Number per Animal Hour	Situations in which aggression occurred		
			Access to Food	Access to Resting Site	Other
I	107	0.29	98	9	-
II	187	0.42	153	10	24
III	109	0.25	84	11	14
IV	191	0.44	128	23	40

Submissive behaviour. Submissive gestures included baring the teeth, with the lips drawn back tightly, rolling up the tail between the hindlegs, and hunching the back. These features are illustrated by the submissive male shown in Plate XVI. They were usually accompanied by the "spat" vocalization described by Jolly as "...a series of high squeaks, given in quick succession..." At low levels of intensity these vocalizations were unvoiced and had the quality of a cat's purr. After giving these signals of submission, the recipient of aggression might remain in his original position or leap off, depending on the persistence of the aggressor and the nature of the previous relationship between them.

Situations in which agonistic behaviour occurred

In all groups, most agonistic encounters occurred in a feeding situation (see Table 17). Typically, the aggressor was feeding and the recipient of aggression approached too close, or the aggressor supplanted the recipient from the latter's feeding station. This contrasts with Jolly's (1966) results: she reported practically no aggressive interactions between animals at Berenty, and only once did she see an aggressive encounter take place with reference to a food source.

Spatial displacements without reference to a food source were rarely seen and occurred only at the onset of resting periods when there was competition for what were presumably preferred resting places. It is probable that I simply failed to see more subtle adjustments of inter-animal distances.

In addition to disputes over access to food and resting sites, there were five other situations in which intra-group aggression was occasionally

observed:

i) the aggressive reaction of Group II's adult female (AQ) to the constant approaches of other group members after the birth of her infant;

ii) her rejection of the Group II juvenile male (J) following the disappearance of her infant when, on three occasions, he tried to suckle from her;

iii) Group IV's adult females' aggressive reactions to adult male R's (AO♂R) attentions in the period preceding the mating season (see Section VIII);

iv) agonistic encounters involving more than two animals. Three instances were observed in Group II: AO♂H cuffed J, who gave a "spat" call and the tense-lipped grin expression, but did not move off, and AQ♀ immediately leapt at AO♂H and pushed him down a vertical trunk until he leapt off. On the second occasion a similar pattern was seen, but this time AO♂H had cuffed YO♂. Thirdly, an apparent case of "redirection" was noted: AQ♀ leapt at AO♂H who spat-called and leapt at YO♂ who immediately left the tree. No triadic interactions were seen in Groups I or III, but an apparent case of redirection was once seen in Group IV when AQ♀ FI approached AO♂R; he exhibited submissive gestures, moved away from AQ♀ FI towards AQ♀ FNI, whom he snapped at and spatially displaced.

v) Forced grooming. This was only observed between AO♂P and AO♂F in Group III. AO♂F frequently approached AO♂P, put his arm round AO♂P's neck and thrust AO♂P's head into the fur on his (AO♂F's) shoulder, forcing AO♂P to groom him. This gesture is referred to as "collaring." AO♂P always responded by grooming AO♂F, with

TABLE 16: Frequency of aggression between members of Group II. Figures in brackets represent number of aggressive encounters recorded during the dry season. Those without brackets represent those recorded during the wet season.

Recipient / Aggressor	♀	♂	YO♂	J	Total
♀	13 (13)	34 (30)	26 (17)		73 (60)
♂		11 (4)	5 (4)		16 (8)
YO♂			10 (16)		10 (16)
J		4 (0)			4 (0)
Total	13 (13)	49 (34)	41 (37)		103 (84)

a full exhibition of submissive gestures.

Frequency of agonistic behaviour

The frequency of agonistic behaviour varied considerably between the four groups, but not consistently between areas (see Table 17). Seasonal variation in the frequency of agonistic behaviour is discussed on P. 256.

Patterns of aggression

Separate analysis of agonistic encounters in the various situations described above give very similar results, so the data are considered together in the following analyses.

Group II. AQ was the only animal in this group who was never the recipient of aggression, and she was also the most frequently aggressive member of the group. AO'H ranked second in that he was never the recipient of aggression from either YO' or J. He was also, after AQ, the most frequent aggressor and the least frequent recipient of aggression in the group. Only between YO' and J, the recipients of aggression in 83.9% of all agonistic encounters, did aggression occur in both directions. The frequency and direction of aggression in this group are shown in Table 18. Results are recorded separately for each season.

Group III. The two adult females, NFD and FD, were never the recipients of aggression from other group members. The outcome of agonistic encounters between them was not predictable, and the encounters were themselves prolonged; the recipient would assume a submissive posture but refuse for up to five minutes to retreat, despite persistent cuffs and bites from the aggressor. These disputes were rare, however, and they were always over access to a feeding station.

TABLE 19: Frequency of aggression between members of Group III. Figures in brackets represent number of aggressive encounters recorded during the dry season. Those without brackets represent those recorded during the wet season.

Recipient	♀NFD	♀FD	♂F	♂P	YO♂	J	Total
Aggressor							
♀NFD	(1)	4	4 (1)	9 (1)	7 (2)		24 (5)
♀FD	1 (2)	3 (5)	1 (3)	2	6 (3)		13 (13)
♂F			17 (5)	9 (1)	12 (1)		38 (7)
♂P				1	1 (2)		2 (2)
YO♂			1		2		3
J					2		2
Total	1 (2)	7 (5)	23 (9)	23 (2)	28 (8)		82 (27)

AO♂F, the recipient of aggression only from the two adult females, was the most frequently aggressive animal in the group. Nearly 58% of all his encounters were with AO♂P.

In 91.8% of the agonistic encounters in which they participated, YO♂and J were the recipients of aggression and in 57% of all agonistic encounters in the group, one of them was the recipient. Although encounters between AO♂P and J were unidirectional (AO♂P was always the aggressor), those between AO♂P and YO♂, and YO♂and J respectively, were uncertain in outcome. Such encounters were rare, constituting only 8.4% of all agonistic encounters.

Full results are shown in Table 19.

Group IV. Observations were made on this group when the two adult females are presumed to have been in oestrus, i.e., during the first week of March. Encounters were recorded at that time whose outcome was the opposite of that in all other months. Taking the data for the other five months, a linear relationship was apparent between AQ♀FI, AQ♀FNI and SA ♂♀, using the direction of aggression to rank them. AQ♀FI was the only individual never subjected to aggression by other members of the group, and she was also the most frequently aggressive animal, initiating 56.5% of all incidents recorded in the group. Of these, 83% were directed at SA ♂♀, AO♂R (January-March) and AO♂INT (April-June).

At the other end of the scale, SA ♂♀, the least commonly aggressive animal, was the recipient in 44% of all the agonistic encounters that occurred in the group. AO♂R was always aggressor in agonistic encounters with AQ♀FNI and SA ♂♀, and he was the second most commonly aggressive animal. However, he was subject to as many attacks from AQ♀FI as AQ♀FNI was from AQ♀FI and AO♂R together. AO♂INT did not subsequently assume this relationship with other group members: he was displaced by AQ♀FNI

TABLE 20: Frequency of aggression between members of Group IV, Figures in brackets represent number of aggressive encounters recorded during the dry season. Those without brackets represent those recorded during the wet season. *These encounters were recorded in March 1971.

Recipient	♀FI	A♂R	♀FNI	SA ♂♀	♂INT	Inf	Total
Aggressor							
♀FI		46	9 (3)	24 (20)	(1)	6	85 (24)
♂R	5*		27	17			49
♀FNI				10 (6)	(3)	2	12 (9)
SA ♂♀	1*	2*	3*				6
♂INT				(6)			(6)
Inf							
Total	6	48	39 (3)	51 (32)	(4)	8	152 (39)

TABLE 21: Contribution of each animal to total group aggression in wet and dry seasons, and Index of Increased Aggression.

Group	Initiator	Contribution to Group Aggression				Index of Increased Aggression
		Wet Season		Dry Season		
		N	%	N	%	
II	♀	73	71	60	83	1.2
	♂	16	15	8	11	2.0
	YO♂	10	10	4	6	2.5
	J	4	4	-	-	-
III	♀FD	13	17	13	48	1.0
	♀NFD	24	29	5	19	4.8
	♂F	38	46	7	26	5.4
	♂P	2	2	2	7	1.0
	YO♂	3	4	-	-	-
	J	2	2	-	-	-
IV	♀FI	85	56	24	62	3.5
	♀FNI	12	8	9	23	1.3
	♂R/INT	49	32	6	15	8.2
	SA♂♀	6	4	-	-	-
	Inf.	-	-	Not present		-

three times and by AQ FI once, and acted as aggressor only in encounters with SA ♂♀.

Full results are shown in Table 20.

Seasonal variation in agonistic behaviour

Aggressive encounters occurred more frequently in the wet season than in the dry. Most animals contributed to this increase, and in not one was a decrease in frequency of aggression recorded. However, the frequency of aggression increased more in some group members than in others. These differential increases were not consistent with any particular age/sex class.

This difference between the two seasons was highly significant (Mann-Whitney U Test using data from Table 21, $N_1=N_2=4$, U=1, $p \leq .01$ - Group II; $N_1=N_2=8$, U=0, $p \leq .001$ - Groups III and IV). Table 22 shows the number of aggressive interactions initiated by members of the study groups in the two seasons. These figures are also expressed as a percentage of the total number of aggressive encounters seen in each group, in each season. This measures each animal's relative contribution to total group aggression. Although most animals contributed to the wet season increase, the Index of Increased Aggression shows that the proportionate increase was higher in some animals than in others. This index is the ratio between the number of aggressive incidents an animal initiates in each season. Where either value is zero, the value of the index must be infinity and is consequently not shown.

Group II. The percentage, or relative, contribution to all aggression increased from dry season to wet season in AO♂ H, YO♂ and J, and dropped in AQ♀. There was, however, a slight real increase in the frequency with which AQ♀ initiated aggressive encounters in the wet season.

Group III. AQ FD's frequency of aggression was consistently high, with a slight increase in the wet season, though her relative contribution to total group aggression dropped in this period. AQ NFD showed a considerable wet season increase both absolutely and in her relative contribution.

AO♂ F's scores showed a wet season increase almost comparable to that of AQ NFD. A significant amount (44.7%) of his aggression was directed at AO♂ P in the wet season (using data from Table 19, X^2=13.69, df=2, p .001). Although in the dry season 71.4% of his aggression was directed at AO♂ P, the sample was too small to test for significance.

AO♂ P showed no change in absolute frequency between seasons, and so his relative contribution fell in the wet season.

Group IV. The data on AO♂ R and AO♂ INT have been combined: this was done in order to provide information on an adult male age/sex class throughout the study period, and it is not implied that AO♂ INT necessarily took over AO♂ R's role in Group IV. (The process of changeover is described in Section VIII.) Both AO♂ R/INT and SA OQ♂ showed large increases in their frequencies of aggression in the wet season. It should be noted that only during the mating season in March did SA OQ♂ initiate aggression against any other member of the group. This was also the only time at which AO♂ R initiated aggression against AQ♀ FI.

The frequency with which AQ♀ FI initiated aggression in the wet season was higher than in the dry season, but her relative contribution to total group aggression nevertheless fell in the wet season. This was also true of AQ♀ FNI.

Description of non-agonistic behaviour

Allo-grooming was the most commonly observed non-agonistic interaction. It could be initiated by the groomer without the groomee necessarily presenting to be groomed. When presentation occurred, the prospective groomee held out an arm towards the prospective groomer, who approached, grasped the arm and began grooming it. In only 10.4% of bouts was grooming concentrated on the limbs. On all other occasions grooming either started on or was transferred almost at once to the head, face and back of the groomee (see Plate XVII). These areas were inaccessible for self-grooming. "Collaring" (see also P.249) of the groomer by the groomee was only observed between adult males F and P in Group III and always resulted in an exhibition of submissive gestures by the groomer, $\vec{\sigma}$P, as he groomed $\vec{\sigma}$F.

All grooming was done by licking with the tongue and scraping the tooth comb over the fur. When grooming the head, the groomer frequently clamped his hand round the groomee's muzzle. 70% of grooming bouts were uni-directional: throughout the bout one animal groomed another. In 4% of bouts, grooming was reciprocal: the two animals involved groomed each other alternately. Reciprocal and simultaneous grooming occurred in 26% of bouts: the animals sat in physical contact, each grooming the other's shoulders or back. This reciprocity developed only after one or the other animal had initiated the bout.

Play behaviour generally involved sub-adults and juveniles, although adults did occasionally join in, and was characterized by the relaxed, open-mouth play face of the participants. In 73% of bouts, participants played on or within 2m. of the ground (see Plate XVIII). Bouts more than 2m. above the ground usually consisted of two or three animals wrestling together, often hanging by their arms or legs alone, each

TABLE 22: Frequency of grooming in Group II. Figures in brackets represent grooming bout frequencies in the dry season. Those without brackets represent frequencies in the wet season.

Groomee / Groomer	♀	♂	YO♂	J	Total
♀		2 (1)	1 (1)	18 (1)	21 (3)
♂	3 (16)		2 (2)	14 (2)	19 (20)
YO♂	3 (12)	4		12 (2)	19 (14)
J	10 (7)	11 (4)	8		29 (11)
Total	16 (35)	17 (5)	11 (3)	44 (5)	88 (48)

trying to dislodge the other(s). Wrestling also occurred on or near the ground, together with chases. Play bouts on the ground frequently culminated in one animal lying on his back with the other repeatedly jumping on to him (see Plate XIX).

Nose-touching was observed as a form of greeting behaviour, as noted by Jolly (1966), but it constituted only 5.7% of all non-agonistic behaviour. The participants approached each other, touched noses briefly and moved apart again. No other form of greeting behaviour was seen, and nose-touching only occurred after long periods of separation.

Situations in which grooming and play occurred

Most grooming occurred during rest periods. The main exception to this was the AO♂F/AO♂P grooming pair. AO♂F might force AO♂P to groom him in any situation if the latter were close to him.

Play behaviour was observed only during the wet season, both in the north and the south, and took place mainly at the beginning and end of feeding and rest periods.

Nose-touching was seen occasionally when animals were reunited after prolonged dispersal of the group during feeding bouts.

Patterns of grooming

Group II. AQ groomed least and was most groomed. She and the juvenile (J) were each groomed more than twice as much as either of the other two group members. 79% of AQ's grooming activity was directed at J.

Full results are shown in Table 22.

Group III. AQ FD and AO♂P both groomed more than any other group member.

TABLE 23: Frequency of grooming in Group III. Figures in brackets represent grooming bout frequencies in the dry season. Those without brackets represent frequencies in the wet season.

Groomee / Groomer	♀FD	♀NFD	♂F	♂P	YO♂	J	Total
♀FD		2 (5)		(1)	2 (1)	6 (3)	10 (10)
♀NFD	2 (3)		2 (1)	1		1	6 (4)
♂F	2 (1)	(1)		(1)	1	3 (5)	6 (8)
♂P		(1)	4 (9)		1	2 (1)	7 (11)
YO♂	2 (1)	1	2 (1)			4 (1)	9 (3)
J	2	2	2 (5)	(1)	1 (1)		7 (7)
Total	8 (5)	5 (7)	10 (16)	1 (3)	5 (2)	16 (10)	45 (43)

TABLE 24: Frequency of grooming in Group IV. Figures in brackets represent grooming frequencies in the dry season. Those without brackets represent frequencies in the wet season.

Groomee	♀FI	♂R/INT	♀FNI	SA♂Q	Total
Groomer					
♀FI		(3)			(3)
♂R/INT	2	1	2		5
♀FNI	10 (5)	1			11 (5)
SA♂Q	3 (6)	(1)	(3)		3 (10)
Total	12 (11)	4 (1)	1 (6)	2	19 (18)

TABLE 25: Frequency of play and nose-touching in Group II. Figures in brackets represent frequency of nose-touching, those without brackets frequency of play.

Initiator / Partner	♀	♂	YO♂	J	Total
♀			1 (1)	1 (1)	2 (2)
♂			3	3	6
YO♂		3		17	20
J	7	7	25 (1)		39 (1)
Total	7	10	29 (2)	21 (1)	67 (3)

In both cases this high frequency of grooming resulted from a special grooming relationship with one other animal in the group, rather than from frequent grooming of every member of the group: 45% of A♀ FD's grooming was directed at the juvenile (J), and 72% of A♂ P's at A♂ F.

A♀ NFD groomed least commonly, and 50% of what grooming she did was directed at the other adult female, A♀ FD.

J and A♂ F were both groomed more than twice as much as any other animal. This was partly due to the special attention that they received from A♀ FD and A♂ P. A♂ P and Y♂ were both groomed much less than other members of the group.

The results are shown in Table 23.

Group IV. A♀ FI groomed least frequently, and the only animal she ever groomed was A♀ FNI. 93% of the grooming initiated by A♀ FNI was directed at A♀ FI. A♂ INT was never seen to groom, or be groomed by, any other animal.

Full results are shown in Table 24.

Patterns of play and nose-touching

Group II. On one occasion J approached Y♂ and they touched noses. A♀ touched noses with Y♂ and J once each.

67 play bouts were recorded. 63% of them were between J and Y♂, and 37% between an adult and J or Y♂. No play uniquely between adults was seen, and J and Y♂ both initiated bouts, and were play-approached more than three times as often as the two adult members of the group. Y♂ participated in more bouts than J, but initiated only 3 (15% of the bouts which he initiated) with an adult - A♂. J initiated 7 bouts (nearly 50% of all the bouts he initiated) with A♂ and A♀ repsectively.

Full results are given in Table 25.

TABLE 26: Frequency of play and nose-touching in Group III. Figures in brackets represent frequency of nose-touching, those without brackets frequency of play.

Initiator / Partner	♀FD	♀NFD	♂F	♂P	♂Y	J	Total
♀FD		1 (2)				(1)	1 (3)
♀NFD	2			1 (1)		1 (2)	3 (3)
♂F				1			1
♂P		(1)		3	1		4 (1)
♂Y	1			1		12 (1)	14 (1)
J			3 (2)	1 (2)	11		15 (4)
Total	3	1 (1)	3 (4)	2 (3)	16	13 (4)	38 (12)

TABLE 27: Frequency of play and nose-touching in Group IV. Figures in brackets represent frequency of nose-touching, those without brackets frequency of play

Initiator	♀FI	♂R/INT	♀FNI	SA♂♀	Inf	Total
Partner						
♀FI		(1)				(1)
♂R/INT			2 (1)	1	1	4 (1)
♀FNI	(1)	(4)		(1)	1	1 (6)
SA♂♀						
Inf				1		1
Total	(1)	(5)	2 (1)	2 (1)	2	6 (8)

Group III. Nose-touching was recorded on 12 occasions and little pattern emerged other than that J was involved in a high proportion (8) of them, and all group members participated at least once (see Table 26).

38 play bouts were recorded. Over half of them were between J and YO♂, 32% between an adult and J or YO♂ and only 7% between adults. Those between adults involved only AQ FD and AQ NFD, and only once did either adult female play with any other animal (one bout initiated by AQ NFD with YO♂). J and YO♂ both initiated many more bouts than other group members did. Of the bouts initiated by J, 4 (26%) were with adult males P or F, whereas YO♂ initiated only 1 (7%) with an adult. 31% of the play-approaches to YO♂ were made by adults, whereas only 8% of those to J were made by adults.

Group IV. Play and greeting behaviour occurred too rarely in this group to suggest any pattern (see Table 27). Nose-touching was seen 8 times. Play was observed 6 times. Three bouts were between an adult and AQ FI's infant, one between AO♂R and SA OQ, and two between AO♂R and AQ FNI. AQ FI was never seen playing.

(N.B. The results presented in the preceding sub-sections are summarized when their significance is considered in the "Discussion and Conclusions" sub-section.)

Seasonal variation in non-agonistic behaviour

The only seasonal variation in the frequency of grooming was found in Group II. Seasonal variation in the frequency of play behaviour was marked in all three groups, however.

In Group II, out of a total of 136 grooming bouts, only 48 occurred

TABLE 28: Contribution of each animal to total frequency of grooming in Group II in wet and dry seasons, and Index of Increased Grooming.

Groomer	Contribution to Grooming				Index of Increased Grooming
	Wet Season		Dry Season		
	%	N	%	N	
♀	24	21	6	3	7.0
♂	21.5	19	42	20	0.95
YO♂	21.5	19	29	14	1.35
J	33	29	23	11	2.63
Groomee					
♀	18	16	73	35	0.46
♂	19	17	10.5	5	3.40
YO♂	13	11	6	3	3.67
J	50	44	10.5	5	8.80

in the dry season. The increase in the wet season was not due to a uniform increase in grooming activity (see Table 28). In the wet season, 57% of all grooming was done by AQ♀ and J, and 90% of the increase in the frequency of grooming was due to them. AQ♀ was the only animal whose grooming frequency declined slightly in the wet season. (This Index is the ratio between the number of bouts observed in the wet season and the number of bouts observed in the dry season.)

In the dry season, AQ♀ and J groomed less than the other two members of the group, and AQ♀ initiated only 6% of dry season grooming. The reverse dituation held for AQ♀ in respect of being groomed: 73% of all grooming was directed at her in the dry season, this figure falling to 18% in the wet season.

Play behaviour was never seen during the dry season in either study area: in the north it was observed only in October, November and December, and in the south in January, February and March. The significance of this seasonal difference is considered in the Discussion sub-section.

DISCUSSION AND CONCLUSIONS

The interpretation of social structure

In early primate studies, the all-inclusive theory of "social dominance" was put forward as the basis of primate social organization (Zuckerman, 1932). This unitary motivational theory postulated that the individuals constituting a social group were ranked in a linear hierarchy, and that the outcome of all interactions was determined by the relative ranks of the animals participating in the interaction. The criteria by which this hierarchy was established included frequency and direction of aggression, preferential access to food sources and

preferential access to receptive females. More recent work has shown that a unitary theory of social structure underestimates the complexity of primate social organizations (Kummer, 1967; Stoltz and Saayman, 1970; Jolly, 1966). In an extensive discussion of the concept of social dominance, Gartlan (1968) pointed out that "...those behaviour patterns which are traditionally associated with dominance...often show no correlation with one another..." He proposed instead to describe the social structure of Cercopithecus aethiops in terms of functional roles played by different members of the group. These roles included territorial display, social vigilance, social focus, friendly approach, territorial chasing, punishing and leading.

Few of the roles envisaged by Gartlan could be differentially applied to members of the P. verreauxi groups studied. However, it would be an oversimplification to revert to the unitary theory of social dominance, and to see all P. verreauxi social relationships solely in the light of a simple linear hierarchy. While the unidirectionality of aggression and displacements in the groups could be used to define a hierarchy in each, there was no consistent correlation between the rank of individuals in a hierarchy established on this criterion and their ranks in hierarchies established according to the frequency of aggression, the direction and frequency of grooming, or preferential access to receptive females.

Feeding hierarchy

Almost all aggressive interactions occurred with reference to access to a feeding station. In the groups in both study areas, a clear-cut hierarchy existed within the context of feeding and, specifically, priority of access to food. This hierarchy is henceforth called the

"feeding hierarchy." In all three groups, the highest ranking animal in the feeding hierarchy was an adult female. Dominance in this hierarchy was not necessarily a function of sex, however: in Group IV, A♂ R always displaced A♀ FNI.

There were only two exceptions to the general rule that agonistic encounters in this context were unidirectional:

1) the two adult females in Group III, who were both unchallenged by other group members, occasionally engaged in protracted aggressive interactions with each other, of unpredictable outcome. This contrasted with the situation in Group IV, where A♀ FI always displaced A♀ FNI.

2) Sub-adult and juvenile animals were always displaced by adults in agonistic encounters, but no stable relationship appeared to exist between the aub-adults and juveniles themselves: aggression between them was two-way.

Outside the context of food, the rigidity of structuring broke down and other factors probably regulated inter-individual relationships. For example, a complete breakdown in structuring occurred in Group IV when the two adult females were in oestrus in March 1971. The significance of this change is discussed in Section VIII.

The role of the mother and her infant

The presence of an infant and associated changes in the behaviour of its mother probably played an important part in regulating social structure within the group.

In both areas, there was an increase in total group aggression during the wet season. In Groups III and IV this was associated with the social disruption of the mating season (see Section VIII), but in Group II the

increase occurred about five months before the mating season. This, together with the fact that the frequency of aggression increased in all but two animals (who maintained their dry season frequencies), suggests that there was some correlation with increased time spent feeding and moving. However, if the increase in aggression were a function of increased feeding and moving alone, it should be uniformly distributed between group members in proportion to previous frequency levels. The data show that this was not the case, and it is postulated that the presence of an infant in Group II contributed to changes in inter-individual relationships.

In the dry season, after the birth of her infant, other members of the group repeatedly tried to approach AQ and to groom or handle her infant. She was frequently involved in aggressive encounters, and in 68% of them her aggression was directed towards animals trying to gain access to the infant. In the wet season, however, 67 out of 73 encounters were over access to a feeding station. It is thus suggested that this protectiveness towards her infant heightened AQ's frequency of aggression in the dry season, so that in the wet season her aggressiveness did not increase proportionately as much as that of other group members.

<u>The role of idiosyncratic relationships</u>

In few field studies have most, or all, members of a group been consistently identified (Jolly, 1966; Van Lawick-Goodall, 1968; Mizuhara, 1964). It has therefore rarely been possible to consider interactions as manifestations of the characteristics of two individual animals rather than as relatively stereotyped encounters between members of age/sex classes. It is possible that social structure, even among pro-

simians, may be partly determined by individual idiosyncracies in addition to predictable patterns of age/sex class interactions.

In Group IV the frequency of aggression was positively correlated with the direction of aggression in the feeding hierarchy, but the data from Groups II and III show that frequency of aggression was not necessarily a correlate of rank. In Group III, AO♂F was the most frequently aggressive animal, although he ranked third in the feeding hierarchy. 49% of his encounters were with AO♂P. This frequent, and often apparently gratuitous, aggression towards AO♂P could be interpreted as an idiosyncratic assertion of dominance in a stable situation, or as an incipient attempt to drive the second male out of the group. The latter interpretation is in line with Petter and Peyrieras' (in press) hypothesis that the family group is the basic unit in the social organization of P. verreauxi, so that symptoms of stress in the form of heightened aggression might be expected when group composition departed from the "norm." However, the evidence for considering the family group as the basic unit of social organization was considered and rejected in Section I, so that AO♂F's behaviour cannot necessarily be considered as a response to the abnormal presence of a second adult male in the group. A detailed study of a much wider sample of relationships between known individuals belonging to different age/sex classes is necessary before it can be definitively established whether the AO♂F/AO♂P relationship reflected individual idiosyncracies or a certain pattern of adult male/adult male interaction.

The dynamics of social structure

Social structure should be considered as a dynamic process and not as a static framework. Some indication of the constantly changing nature

of social groups has been given by long-term studies of baboon, chimpanzee and Japanese macaque populations (Rowell, 1969; Van Lawick-Goodall, 1968; Itani, 1963; Mizuhara, 1964). Thus in a given group certain relationships may in the short-term appear stable although they are in fact undergoing a gradual change. This may have been true of the YO♂/J relationship in Group II. YO♂ was more frequently aggressive than the adult male, AO♂H, although the latter ranked higher in the feeding hierarchy. However, all of YO♂'s aggression was directed at J, whereas J initiated aggression towards, and displaced, YO♂ only four times. It is possible that YO♂, the older of these two immature animals, was in the process of changing the existing two-way relationship, involving reciprocal initiation of aggression and frequent play bouts in the wet season, into the dominant/subordinate relationship characteristic of the adult feeding hierarchy. It is postulated that AO♂H was less often aggressive because his position had only to be maintained rather than established.

Grooming behaviour

Adult females generally initiated less grooming, and were more commonly groomed, than other members of their groups. This suggests a positive correlation between groomee frequency and rank in the feeding hierarchy. In a review paper, Sparks (1967) notes that "...the majority of the allogrooming bouts in Old World primates are against the dominance slope of the hierarchy prevailing in these communities..." However, despite this tendency for dominant animals to groom least and be groomed most, the existence of frequent grooming as a function both of maternity and of harassment of one animal by another complicated relationships and removed the simple linearity of the feeding hierarchy. 79% of the

grooming initiated by AQ in Group II was directed at J, and in Group III many of the numerous bouts initiated by AQ FD were directed at J (and at the co-dominant AQ NFD). AO♂P and YO♂ in Group III were, predictably, rarely groomed by other animals. However, most of AO♂P's grooming was directed not at the two most dominant females, but at AO♂F.

Predictions based on the analysis of data from the other groups are confirmed in Group IV. In this group, with no juvenile and only one fully adult male present at any one time, the simple linearity of the feeding hierarchy was reflected in the frequency and direction of grooming bouts.

Play bouts

Play bouts were commonest between sub-adults and juveniles and rare, or absent, between adults. Although no adult-adult play bouts were observed in Group II, there were nonetheless many more bouts between immature animals than between any animals in either of the southern groups. The absence of play between adults was a group-specific occurrence, in that it was frequently recorded in the wet season among Group I adults.

The apparent discrepancy between play frequencies in Groups III and IV was probably due to the lack of peers for the Group IV infant. Taking only adult-adult and adult-infant figures for Group III and comparing them with Group IV figures, corrected for group size, there was little difference in bout frequencies. More difficult to understand was the discrepancy in the frequency of play between seasons, in both study areas: in neither area did animals play during the dry season. The reason for this is not known, but may be related to restrictions in activity due to reduced availability of energy.

SUMMARY

1) In this Section, a detailed account of intra-group relationships outside the mating season was given. The analysis was based on data collected for Groups II, III and IV on agonistic and friendly behaviour.

2) An animal that displaced, threatened, bit or cuffed another animal in its own group was considered to be the aggressor in an agonistic encounter.

3) Submissive gestures included baring the teeth, rolling up the tail between the hindlegs, and hunching the back.

4) In all groups, most agonistic encounters occurred in a feeding situation, and spatial displacements without reference to a food source were rarely seen. Aggression was also commonly seen when animals tried to handle a mother's infant - the mother would cuff and bite them to prevent them gaining access to her infant. A few instances of probable re-direction of aggression were noted.

5) The frequency of agonistic behaviour varied considerably between the four groups, but not consistently between areas. Aggressive encounters occurred more frequently in the wet season than in the dry, in all four groups. Most animals contributed to this increase, and in not one was a decrease in frequency of aggression recorded. However, the frequency of aggression increased more in some group members than in others.

6) Allo-grooming was the most commonly observed non-agonistic interaction. Most areas groomed were inaccessible for self-grooming. All grooming was done by licking with the tongue and scraping with the tooth comb. Bouts might be unidirectional, reciprocal, or reciprocal and simultaneous.

7) Play behaviour generally involved sub-adults and juveniles, although

adults did occasionally join in, and was characterized by the relaxed, open-mouth play face of the participants. Nose-touching was a rarely observed form of greeting behaviour.

8) Most grooming occurred during rest periods. Play behaviour was observed only during the wet season, and took place mainly at the beginning and end of feeding and rest periods. The only seasonal variation in the frequency of grooming was found in Group II; more grooming took place in the wet season.

9) The unitary theory of social dominance underestimates the complexity of primate social organizations. Gartlan proposed that the concept of roles should be substituted for that of dominance. Few of the roles he envisaged could be differentially applied to members of the P. verreauxi groups studied. However, it would be an oversimplification to see all P. verreauxi social relationships solely in the light of a simple linear hierarchy. Unidirectionality of aggression and displacements in the groups could be used to define a hierarchy in each, but there was no consistent correlation between the rank of individuals in a hierarchy established on this criterion and their ranks in hierarchies established according to the frequency of aggression, the direction and frequency of grooming, or preferential access to females.

10) A clear-cut hierarchy existed with respect to access to food. This was called the "feeding hierarchy." In all three groups, the highest ranking animal in the feeding hierarchy was an adult female. Dominance in this hierarchy was not necessarily a function of sex, however.

11) The presence of an infant and associated changes in the behaviour of its mother probably played an important part in regulating social structure within the group. It is suggested that the mother's protectiveness towards her infant heightened her frequency of aggression

in the dry season, so that in the wet season her aggressiveness did not increase proportionately as much as that of other group members.

12) It is postulated that social structure may be partly determined by individual idiosyncracies in addition to predictable patterns of age/sex class interactions; the frequent, and often apparently gratuitous aggression of AO♂F towards AO♂P could be interpreted as an idiosyncratic assertion of dominance.

13) Social structure should be considered as a dynamic process and not as a static framework. In a given group certain relationships may in the short-term appear stable although they are in fact undergoing a gradual change.

14) Adult females generally initiated less grooming, and were more commonly groomed, than other members of their groups. This suggests a positive correlation between groomee frequency and rank in the feeding hierarchy. Despite this tendency for dominant animals to groom least and be groomed most, the existence of frequent grooming as a function both of maternity and of harassment of one animal by another complicated relationships and removed the simple linearity of the feeding hierarchy.

15) The discrepancy in the frequency of play between seasons, in both study areas, was not understood, but may be related to restrictions in activity during the dry season due to reduced availability of energy.

SECTION VIII: PATTERNS OF MATING

INTRODUCTION

A description of activities during the mating season is presented in this section, indicating the extent to which they differed from activity patterns during the rest of the year. An attempt is then made to interpret the significance of these results as part of a total pattern within the context of group social organization. Since the results from the two southern groups were highly diverse, the final evaluation is tentative. I was not present during the mating season in the north: in all Malagasy prosimians, mating appears to be seasonal under natural conditions, and in P. verreauxi the timing of the birth periods showed that mating must occur during January, February or March all over the island.

As far as possible, the quantitative record of activities was maintained during the mating season, but it was complemented by extensive descriptive notes on the many activities observed at this time that fell outside the scope of the data sheet.

RESULTS

Nature of behavioural changes in the pre-copulatory period

Slight flushing of AQ FNI(IV)'s[1] vulva coincided with a sudden, significant increase in certain activities in Group IV in late January 1971. Similarly increased frequencies were noted throughout February and during the first ten days in March, although there was no

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[1]The age-class of the animal referred to is henceforth omitted, and the group to which it belongs has been added in brackets after the identifying initials.

TABLE 29: Changes in frequency of endorsing in Groups III and IV. Figures are expressed as a frequency per adult male hour; only data recorded when an adult male was the day's subject were used in calculations.

Group	Jan 1971 Vulval Change		Feb 1971	March 1971	April 1971	Sept. 1971
	Pre-	Post-				
III	1.95	-	2.35	1.08	0.67	1.41
IV	1.90	6.75	6.26	7.00	1.04	-

visible unusual coloration of either female's vulva in Group IV at this time. Copulation took place in March, and the six weeks preceding it are henceforth referred to as the pre-copulatory period.

The five activities described below occurred occasionally throughout the year, but only in the mating season were they common. The emphasis is thus upon a quantitative rather than a qualitative change in behaviour during these months. In the description below, where no figures are quoted it is to be assumed that no change was found. It should be noted at this point that although there were striking discrepancies between the data collected on each group throughout the mating season, infants were born to known females in both Groups III and IV in August 1971. (The implications of this are discussed later.)

1) <u>"Endorsing" by adult males</u>. Although adults of both sexes scent marked in a number of contexts (further discussion in prep.), during the pre-copulatory period there were increases only in scent marking by males. Females marked either by rubbing the ano-genital region, or by urinating, on a trunk or branch; marking by adult males might include rubbing a branch or trunk with the scent gland located on the ventral surface of the throat (see Plate XX), then with the tip of the penis, usually urinating slightly as this was done, and finally with the perineal area (see Plate XXI). Although an adult male might perform any one part of this sequence when marking, the whole sequence was commonly performed together. Both sexes had a highly developed, almost tubular perineal area. The term "endorsing" was applied when a male marked a spot within five minutes of a female having marked there. Frequency changes in endorsing are shown in Table 29. The figures for Group IV showed a large increase in frequencies in the mating season, but those for Group III showed little variation.

2) "Sniff-approach and mark" by adult males. This occurred when an adult male approached a female and marked the tree trunk just below her tail: the male climbed the trunk under the female and touched her anus with his nose. He then throat marked, and finally marked with his ano-genital area. This sequence was frequently incomplete, for the female might lunge at the male as he thrust his nose under her tail, forcing him to retreat without marking: in such cases endorsing usually followed when the female moved off.

Summing the data, sniff-approach and mark sequences were recorded six times in 216 hours of quantitative observation of Group IV outside the pre-copulatory period. The sequence was observed (in complete or incomplete form) 65 times in 216 hours between January 24th and March 15th 1971.

3) "Roaming" behaviour. Evidence from the study group males and from the arrival of unknown males in the study area, indicated an increase in male "roaming" behaviour at this time: males, singly or in pairs, detached themselves from their own groups and made long forays into the home-ranges of other groups. 23 such excursions were observed during the mating season, involving males from Groups III and IV. Sometimes this behaviour culminated in fierce fights between adult males and in copulation with adult females in the groups encountered.

During the rest of the study, no solitary or paired males were encountered in the home-ranges of the study groups. On only four occasions was an adult male from Group III or IV recorded as probably being out of immediate audio-visual contact with all other members of his group for over two hours. However, since it was usually the absence of these animals that was noticed, it was rarely possible to confirm that they had detached themselves from the group rather than moved to rest in a position out of my sight.

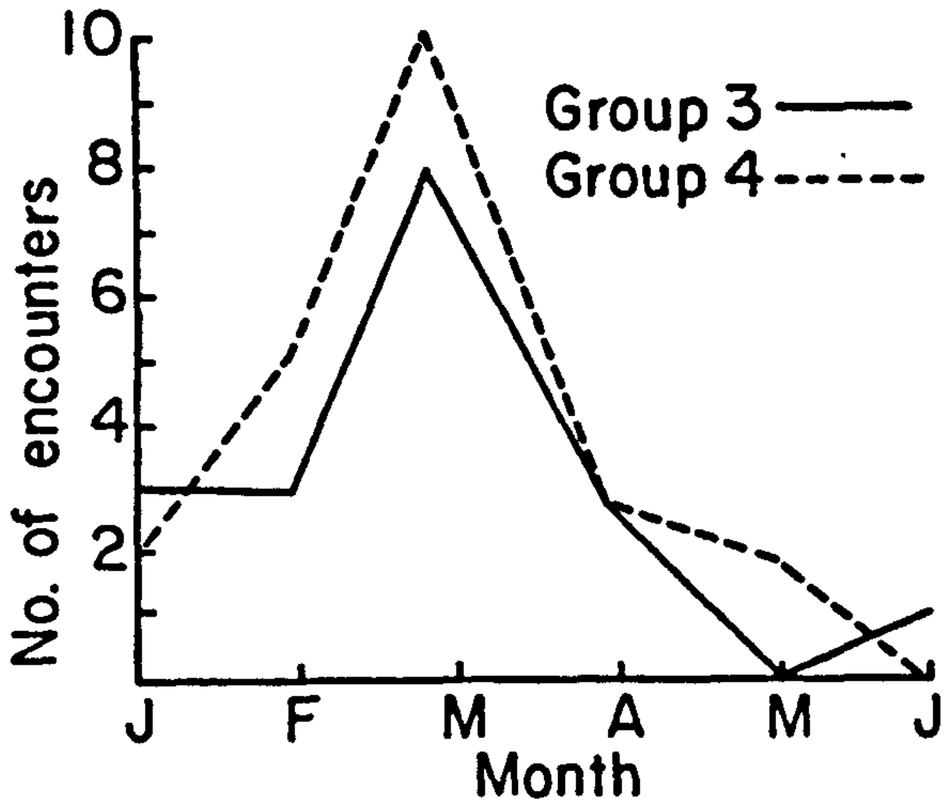
4) Intra-group agonistic encounters. Certain features of intra-group aggression changed during the mating season: there was a highly significant increase in the frequency of aggressive encounters in both Groups III and IV during the mating season. Although most animals contributed to this increase (see Table 21), the Index of Increased Aggression showed that the proportionate increase was higher in some animals than in others. ("Dry season" in Table 21 can be equated with "non-mating season" and "wet season" with "mating season.")

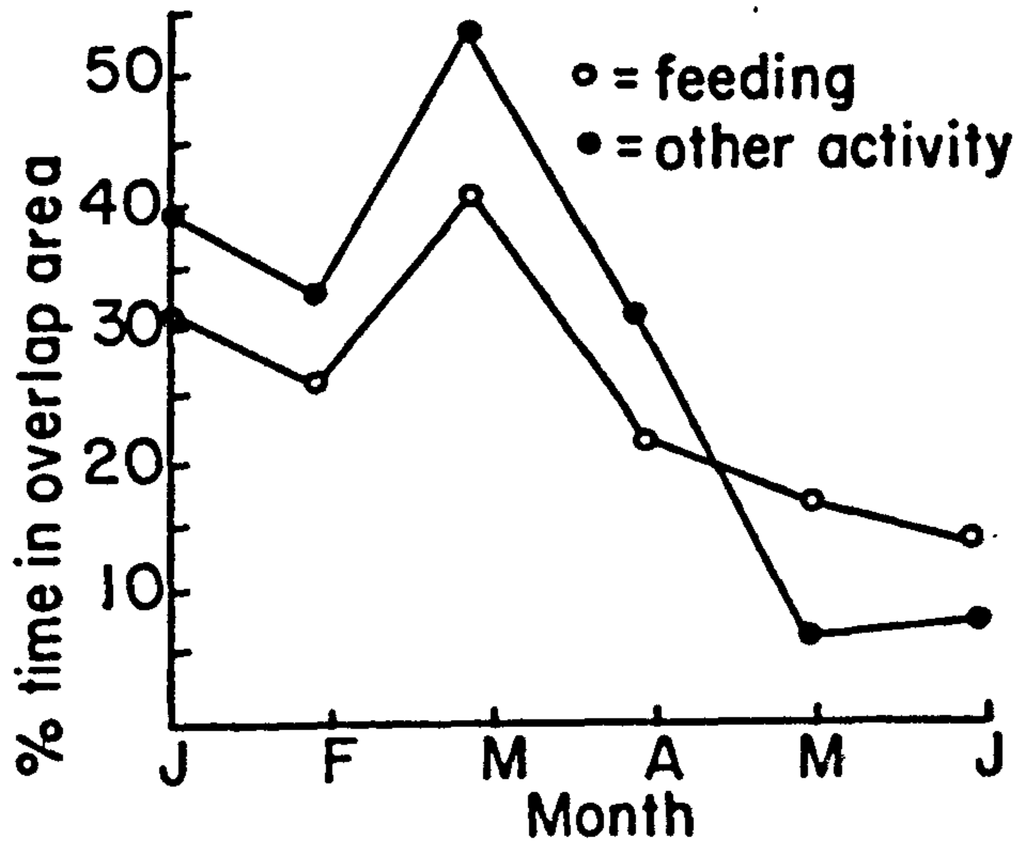
In Group III the highest proportionate increase was seen in $\vec{\sigma}$F. Comparison of the combined frequencies for $\vec{\sigma}$R(IV) and $\vec{\sigma}$INT(IV) between the mating and non-mating season showed much higher frequencies during the mating season. It should be noted that there was no frequency increase in $\vec{\sigma}$P(III), but that there was a substantial increase in $\vec{\sigma}$Q(IV), although an index could not be calculated.

Recapitulating on Section VII, a linear dominance, or feeding, hierarchy could be determined incorporating all adults. The hierarchy was defined using agonistic encounters over access to feeding stations. The initiation of aggression and displacements were found to occur consistently in one direction. During the copulatory period, a break-down in this non-mating season (N.M.S.) feeding hierarchy occurred in Group IV. Although $\vec{\sigma}$Q, an immature subordinate male, took little part in events during the period of copulation, it was the only time when he was seen initiating aggression against other members of the group. This period was also associated with persistent invasion of Group IV by "roaming" males (see below). In Group III, $\vec{\sigma}$F retained his position as N.M.S. dominant male, unchallenged by intruders, and no reversal was seen in the linearity of the N.M.S. dominance hierarchy, nor was there any increase in aggression by subordinate $\vec{\sigma}$P within the group.

Fig. 39. Changes between months in the frequency of inter-group encounters for each group in the southern study area.

Fig. 40. Changes in their allocation of time to different activities in the area of overlap during the mating season by Group III.


10
8
6
4
2
No. of encounters
Group 3
Group 4
J
F
M
A
M
J
Month


50
40
30
20
10
% time in overlap area
o = feeding
• = other activity
J
F
M
A
M
J
Month

5) Inter-group encounters. During the pre-copulatory period and the mating season, Groups III and IV were both involved in many more encounters with neighbouring groups than during subsequent months. The difference was highly significant (Mann-Whitney U test, $N_1=N_2=3$, U=0, $p \leq .05$). Figure 39 shows this change in the frequency of inter-group encounters for each group.

During the pre-copulatory period and mating season, 79% (11/14) of Group III's encounters were with Group IV, and 65% (11/17) of Group IV's encounters were with Group III. Since the home-ranges of at least two groups in addition to Group IV's were known to lie alongside that of Group III, and of at least three in addition to Group III's alongside that of Group IV, the frequency of Group III/IV interactions was very high, assuming that all neighbouring groups should interact equally often. There was no difference between the frequencies with which Groups III and IV interacted with their various neighbouring groups after the mating season. It is thus unlikely that my presence accounts for the discrepancy during the mating season, in that I was equally likely to inhibit the approach of unhabituated neighbouring groups throughout the study.

This specific increase in the frequency of encounters between Groups III and IV is unlikely simply to have been a function of increased food availability in the overlap area of their home-ranges resulting in both groups spending longer in this area. The Group III/IV overlap area was a strip about 100m. wide, running about 150m. along the edge of the home-ranges of the two groups; it constituted approximately 5% of the home-range of each group. Group III spent more total time in the overlap area during the pre-copulatory period and the mating season than in subsequent months, but their allocation of time to different activities did not increase uniformly. This is shown in Figure 40. During the pre-copulatory period and mating season, 56% of the time Group III spent in

the overlap area was devoted to activities other than feeding. This dropped to 38% after the mating season. Thus the results suggest that Group III was spending long periods in the overlap area not simply because there was abundant food there, but rather because they were involved in other activities there; further, neither the vegetational analysis nor subjective impressions indicated that there was in fact an increase in food availability in that area at that time. Evidently, the results cannot be conclusive: in causal terms, it is possible that Group III entered the overlap area because of an abundance of food there, and that ensuing encounters with Group IV were incidental, although they did reduce the amount of time available for feeding.

Considering Group IV, only in January was significantly more time spent in the overlap area: when the January data are excluded, no significant difference remained between the other months (Kruskal-Wallis One-Way Analysis of Variance, N=30). There was no significant difference in the proportion of time this group spent in feeding and activities other than feeding between the pre-copulatory period and mating season, and subsequent months (Mann-Whitney U test, N=36).

Throughout the study there was a highly significant difference between the amount of time each group spent in the overlap area (Mann-Whitney U test, $N_1=N_2=6$, $U=0$, $p \leq .01$), Group IV spending much less time there than Group III.

No pattern of inter-group dominance emerged from inter-group encounters (in prep.). Group III did consistently spend longer than Group IV in the overlap area, particularly during the pre-copulatory period and mating season. The latter increase was associated with a disproportionate increase in activities other than feeding by Group III, and with an increased frequency of encounters between Groups III and IV. Thus, although a close association was apparent between the two groups during

the mating season, the mechanisms bringing it about remain obscure.

Description of behavioural changes in the pre-copulatory period

The following account is of daily behavioural changes seen during the pre-copulatory period. Where no comment is made it can be assumed that activities were similar to those seen outside the mating season. Changes seen in Group IV are considered first.

Observation of Group IV was begun on January 18th: in the following six days, ♂Q(IV) was twice absent from the group for over two hours.

January 24th: ♂R(IV) endorsed after ♀FNI(IV) nine times. On the four occasions he tried to sniff-approach and mark under ♀FI(IV), she lunged at him and he retreated.

January 25th: ♂R(IV) endorsed seven times after ♀FI(IV) and 11 times after ♀FNI(IV). There were five incomplete sniff-approach and mark sequences between ♂R(IV) and ♀FI(IV).

January 26th: ♀FNI(IV)'s vulva was slightly flushed. ♂Q(IV) was found sleeping beside a strange male, ♂INT, near the two females. This male, who had occasionally been seen with the group in September 1970, disappeared as soon as the group moved off. ♂Q(IV) spent most of the day away from the group, and ♂R(IV) left it twice; the second time, he encountered Group III in the III/IV overlap area and headed straight for ♀FD(III) until intercepted and chased away by SA ♂Y(III). ♂R(IV) left after three such attempts to reach ♀FD(III). ♂R(IV) endorsed 63 times after ♀FI(IV) and ♀FNI(IV). (Marking continued throughout the day, where in other months no marking was seen after 1430h.) Two incomplete sniff-approach and mark sequences were seen between ♂R(IV) and ♀FI(IV). Five complete sequences were seen between ♂R(IV) and ♀FNI(IV).

January 27th: ♀FNI(IV)'s vulva was still flushed. ♂R(IV) left the group

and returned to the locality of his encounter with Group III on the 26th, but did not make contact with Group III. ♂INT approached the group and ♀FNI(IV) marked beside him; he sniff-approached and marked under her once. ♂R(IV), having lunged at ♂INT when he first appeared, then moved away and only rejoined the group when ♂INT moved off.

January 28th: ♀FNI(IV)'s vulva was no longer flushed. Endorsing and sniff-approach and mark frequencies were at a post-mating season level.

February 6th: ♂R(IV) had lost large chunks of fur. ♂Q(IV) moved peripherally to the group and then approached with ♂INT. The latter moved away again at once. Endorsing frequency by ♂R(IV) was high, but no sniff-approach and mark sequences were seen.

February 7th: ♂R(IV) chased ♂INT away from the group 3 times, each chase ending in a fight.

February 8th: ♂Q(IV) left the group at midday and was found in the evening grooming an unknown male, ♂LCE, 10m. from Group IV. ♂LCE moved off as I approached and ♂Q(IV) stayed with the group. Incomplete sniff-approach and mark sequences were seen three times between ♂R(IV) and ♀FI(IV).

February 13th: Group IV were found sunning themselves with ♂LCE and two other unknown females. The three unhabituated animals fled when they saw me.

Cyclonic rain cut off access to the study area for the following seven days.

February 20th: ♂R(IV) and ♂Q(IV) were found in the middle of Group III's home-range, but no interaction with Group III was seen. ♂R(IV) endorsed after ♀FI(IV) and ♀FNI(IV) 61 times. 11 complete sniff-approach and mark sequences between ♂R(IV) and ♀FNI(IV) were seen, and 4 incomplete ones between ♂R(IV) and ♀FI(IV): the latter cuffed and bit ♂R(IV), as she did earlier in the month and in January; but for the first time, ♂R(IV)

did not retreat in the face of this aggression.

February 22nd: ♂R(IV) endorsed 35 times in three hours' observations.

Thus, in summary, this period was notable in Group IV for the brief flushing of ♀FNI's vulva, the heightened frequencies of endorsing and sniff-approach and mark sequences by ♂R, and the frequency of roaming, both in non-group and group males. Changes of this nature were absent in Group III, with two exceptions: twice during February, ♂P(III) spent whole days away from Group III.

Description of behavioural changes and copulation in March 1971

Copulation was said to have occurred when intromission took place. Mounting with no intromission is described separately. It was impossible to determine reliably when ejaculation occurred. Copulation by three males with the two females in Group IV was observed between March 3rd and 6th. This was the only period during the field study when male/male and male/female mounting was observed, and on only two other occasions were males observed with erections: once during an inter-group interaction, and once during a play bout between a sub-adult and juvenile.

During the first observed mounting, ♂F grasped ♀FI with his hands around her legs, which were doubled up in a squatting position (all copulation took place on vertical trunks), and he held the trunk below the female with his feet. She curled her tail up and held it slightly to one side during copulation. In subsequent mountings, there was some variation in posture, with the male grasping the female by her upper arms with his hands, and by her doubled-up legs with his feet.

The frequencies of the five activity patterns described above, namely, endorsing, sniff-approach and mark sequences, roaming behaviour, inter-male aggression, and inter-group encounters, reached a peak during the

four days when copulation occurred with Group IV females FI and FNI. The following account details events during this period.

March 3rd: After a brief early morning interaction with a group to the south, Group III fed, steadily moving west until 0945h. when they encountered Group IV. An extract from field notes is given below to describe the subsequent sequence of events.

0954h. A characteristic inter-group confrontation begins between Groups III and IV. ♀FNI(IV) is not present.

0955h. ♂F(III) mounts ♀FI(IV); he dismounts almost at once and joins in the general chasing (characteristic of most group confrontations).

0956h. ♂F(III) mounts ♀FI(IV) again, but dismounts at once to chase ♂R(IV).

1001h. ♀FI(IV) is grasping a vertical trunk, with ♂P(III), ♂F(III), ♂R(IV) and SA ♂Y(III) sitting on the ground in a circle round her. Each male tries to approach her but she repels them by slapping, lunging or biting them. The rest of Group III are feeding 10m. away.

1005h. ♂R(IV) lunges at ♂F(III) who moves off, followed at once by ♀FI(IV). The other three males follow her.

1009h. ♂F(III) mounts her on a vertical trunk but SA ♂Y(III) approaches and bites ♂F(III)'s tail. He dismounts and chases SA ♂Y(III) down the trunk. This happens twice more.

1014h. ♂F(III) mounts ♀FI(IV) and apparently ejaculates after 24 thrusts. No more than six consecutive thrusts had occurred in earlier mountings and it was uncertain whether there was intromission. The other three males sit watching. ♂F(III) then dismounts and sits beside ♀FI(IV) licking his genitalia.

1017h. ♂R(IV) sniff-approaches and marks under ♀FI(IV), and then chases ♂P(III) and SA ♂Y(III).

1029h. ♀FI(IV) leaps off followed by ♂F(III). She cuffs him and he leaps off and is chased by ♂R(IV). ♂R(IV) then chases ♂P(III) away. ♂R(IV) sniff-approaches and marks under ♀FI(IV) and she leaps off, closely followed by ♂R(IV) and at a distance by ♂F(III), ♂P(III) and SA ♂Y(III).

1035h. ♀FI(IV) sits self-grooming beside ♂R(IV). ♂P(III) and SA ♂Y(III) are 5m. away and ♂F(III) much further still. ♂R(IV) tries to mount ♀FI(IV) and she cuffs him and moves off north followed by him. ♂P(III) and SA ♂Y(III) immediately endorse the sitting-place she has just left.

1045h. ♂F(III) has moved off and is feeding with ♀FD(III) and ♀NFD(III).

This sequence was typical of the copulatory period, with one or other female acting as a focus for male attention, yet rejecting the majority of male advances, and with persistent inter-male aggression. However, it was the only time a male was seen to mount and copulate with a female, without first winning a prolonged and fierce bettle with another male.

During the rest of the day, on March 3rd, ♂P(III) followed Group IV; he was chased away 47 times by ♂R(IV), and several of these chases terminated in fights. SA ♂Y(III) stayed with ♂P(III) until midday, and then returned to Group III. ♂P(III) mounted SA ♂Y(III) three times while they were trailing Group IV together, and each time SA ♂Y(III) snapped and wriggled to free himself. This was the only occasion when male-male mounting was seen. Twice, ♂R(IV) tried to mount ♀FI(IV) and each time she snapped and wriggled and escaped.

Checks on Group III indicated that group activities were normal.

March 4th: SA ♂Y(III) and ♂P(III), both in good condition, were found near Group IV. In contrast, ♂R(IV) had lost large chunks of fur and had two long gashes on his thighs. Between 0600h. and 1030h., nine incomplete sniff-approach and mark sequences were seen between ♂R(IV) and ♀FI(IV); ♂R(IV) also chased and fought ♂P(III) 45 times, and ♂Q(IV) did so eight times. However, ♂R(IV) slowed up and tired visibly, and at 1030h. ♂P(III) chased ♂R(IV) from the group. The latter retreated very slowly and quadrupedally across the ground. This was the only time an animal was ever seen moving quadrupedally on the ground. After a brief period of reciprocal chasing between ♂P(IV) and ♂P(III), ♂Q(IV) on his own did not chase ♂P(III) again. At 1136h. ♀FI(IV) leapt over to ♂P(III) and they touched noses.

That afternoon, ♀FI(IV) moved on to a vertical trunk just above ♂P(III)'s head and rolled her tail up. He mounted her and thrust slowly

for about one minute, and then dismounted to chase ♂Q(IV) away. Two further mountings were similarly interrupted, but finally he remained on the female for approximately four minutes, thrusting about 40 times. After this, when ♂P(III) tried to approach, both ♀FI(IV) and ♀FNI(IV) started cuffing and biting. ♂Q(IV) remained on the periphery of the group, alternately approaching and being chased away by ♂P(III). At 1742h., ♂P(III) chased ♂Q(IV) west, where ♂R(IV) was found feeding: ♂R(IV) and ♂Q(IV) fled together. ♂P(III) mounted ♀FI(IV) once more, but there was no intromission and he leapt off almost at once to chase ♂R(IV) and ♂Q(IV).

March 5th: ♀FI(IV) and ♀FNI(IV) and ♂Q(IV) were found together, the latter with a swollen lower lip and a small cut on his arm. Neither ♂P(III) nor ♂R(IV) were present, and ♂P(III) was not seen again until March 10th. In the late afternoon ♂R(IV) appeared and ♀FNI(IV) leapt over and touched noses with him briefly; ♂R(IV) then approached ♂Q(IV) and presented for grooming. ♂Q(IV) spat-called and groomed ♂R(IV) briefly but suddenly appeared to start grappling with him; one of the two screamed and ♂R(IV) leapt off at once. ♂Q(IV) followed, but as he approached ♂R(IV) tail-rolled, spat-called and leapt away. ♂R(IV) did not approach the group again. That evening ♂INT approached the group and ♀FNI(IV) sexually presented to him (i.e., stationed herself on a vertical trunk just above his head and rolled her tail up). He mounted her and 53 thrusts were counted in four minutes before he dismounted. As after previous incidences of prolonged copulation, the two animals sat near each other licking their own genitalia.

March 6th: ♂INT mounted ♀FNI(IV) three times in the early morning, twice dismounting to chase ♂Q(IV). This was the last time mounting was seen. ♂LCE appeared but was chased away by both ♂INT and ♂R(IV). ♀FI(IV) and ♀FNI(IV), and ♂INT and ♂Q(IV) moved together all day; ♂R(IV) moved

peripherally, retreating when any other animal came near him. Once, ♂Q(IV) groomed ♂INT briefly: ♂INT spat-called and tail-rolled as ♂Q(IV) appraoched.

March 7th: An intergroup encounter, typical of those seen outside the mating season, took place between Groups III and IV (the latter group comprising ♂INT, ♂Q, ♀FI and ♀FNI).

March 10th: ♂P(III) rejoined Group III, with an injured nose: the nasal bones had been exposed, but the flesh still hung from his nose on a piece of skin; he persistently, but unsuccessfully, tried to lick his nose, and once licked his hand and then put it to his nose. After suppurating for two or three days, the wound began to heal and within a month it had healed totally, leaving him with flattened facial features and a wheeze as he breathed (see Plate XXII). Throughout the 10th, and most of the 11th, ♂P(III) moved away if approached by any member of Group III. On the evening of the 11th, however, ♂P(III) entered a tree where the juvenile was feeding; they touched noses, and ♂P(III) began feeding in the same tree.

March 12th: ♂R(IV) approached J(III), who rapidly retreated towards other members of Group III, and SA ♂Y(III) chased ♂R(IV) away.

March 13th, 14th, 15th: ♀FI and ♀FNI and ♂INT and ♂Q moved as a well-integrated group, and this composition was retained until observations ended in September 1971. ♂R(IV) intermittently moved on the periphery of the group; he retreated from ♂INT, but was not chased by him. ♂LCE also moved peripherally to the group, attempting to approach the adult females; he was chased away by all group members and was not seen when observations were resumed in April.

The study area was abandoned on March 16th because of local political unrest. When observations were resumed in mid-April, ♂R(IV) had disappeared and ♂INT had largely taken over his role in Group IV. ♂P(III)

TABLE 30

	PRE-COPULATORY PERIOD		COPULATORY-PERIOD	POST-COPULATION
	January 24-31st	February 1st-13th	February 20-28th	March 3-6th	March 7-15th
Vulval flush	Present in ♀FNI (IV) on 26th and 27		-	-
Endorsing	High frequency in ♂OR(IV)		High frequency in all adult males studied	-
Sniff-approach and mark sequences	High frequency in ♂OR(IV)		High frequency in all adult males studied	
Roaming (movements by adult males)	1) ♂INT approaches Group IV twice 2) ♂♀Q(IV) leaves Group IV 3 times 3) ♂OR(IV) leaves Group IV 3 times (once to approach Group III)	1) ♂ INT approaches group IV twice 2) ♂LCE approaches Group IV twice (3) ♂♀Q(IV) leaves Group IV once.	1) ♂♂OR(IV) and ♀Q(IV) leave Group IV and make a foray into home range of Group III 2) ♂OP(III) leaves Group III twice	1) SA♂Y(III) approaches and follows Group IV 2) ♂OP (III) approaches & follows Group IV-mates. 3) ♂ INT sp-proaches & follows Group IV - mates. 4) ♂LCE approaches & follows Gr. IV - is chased away. 5) ♂OR(IV) ousted from Group IV by ♂OP(III) and ♂ INT in turn	1) ♂OP(III) rejoins Group III 2) ♂OR(IV) approaches Gr. III - is chased away 3) ♂LCE approaches Gr. IV- is chased away

TABLE 30 (Cont.)

	PRE-COPULATORY PERIOD			COPULATORY-PERIOD	POST-COPULATION
	January 24-31st	February 1st-13th	February 20-28th	March 3-6th	March 7-15th
Intragroup High frequency agonistic in both groups encounters					
Intergroup High frequency encounters in both groups				[♂F(III) mates with ♀FI (IV) during inter-group encounter on March 3rd]	
Copulation	-	-	-	(In order of occurrence) ♂F(III) with ♀FI (IV) ♂P(III) with ♀FI (IV) ♂Int with ♀FNI (IV)	

had resumed his former position as subordinate male in Group III.

A summary of events in this, and the pre-copulatory period, is given in Table 30.

DISCUSSION AND CONCLUSIONS

Petter-Rousseaux(1962) has shown that, in the laboratory, the Cheirogeleinae are seasonally polyoestrus. Lemur catta is also seasonally polyoestrus in captivity, non-pregnant females cycling three times (Evans and Goy, 1968). Jolly (1966) produced evidence for L. catta in the wild having a "pseudo-oestrus period" approximately one month earlier than the true breeding season: the vulval area of four or five of nine females went through a pink phase 3 - 4 weeks before the week of mating, which faded and then flushed again just prior to mating. Two of these females were seen mating in the second period of flushing.

Data from Group IV in this field study indicate that P. verreauxi do not have more than one full oestrus period in the breeding season, but that there was a period analagous to Jolly's "pseudo-oestrus period" in L. catta. It is suggested that the flushing of QFNI(IV)'s vulva and associated activities, in late January, represented a partially suppressed oestrus 37 days before full oestrus. This did not occur in Group III despite the presence of two adult females and it seems likely that the suppression was total in this group: between January 14th and February 13th no more than three consecutive days passed without observations being made on Group III so it is unlikely that, if it occurred, a "pseudo-oestrus period" would not have been seen. Both females in Group III probably came into full oestrus once, at the same time, either between the 13th and 20th of February, or after the 15th of March.

The timing of births provides further evidence for the extreme seasonality of breeding in P. verreauxi, in that it should reflect the

incidence of female receptivity in the mating season, and the degree of synchronization between females. P. verreauxi has a gestation period of about 130 days (Petter-Rousseaux, 1962). The length of the oestrus cycle is not known, but it is reasonable to assume that it is of approximately the same duration as that of L. catta in captivity; this lasts 39.3 days, with a range of 33 - 45 days (Evans and Goy, 1968). If females in the study groups had been polyoestrus with a fully synchronized cycle similar in length to that of L. catta, two birth peaks might have been expected, the second about five weeks after the first, when females fertilized during the second oestrus period gave birth. However, extrapolating from the birth-period evidence in the wild, there was only one full oestrus period with considerable synchrony between females, during which all mating and fertilization took place: at Ampijoroa in the north of Madagascar, births of P. v. coquereli were scattered over a maximum of 21 days in 1970 and 1971. Jolly (1966) reported a ten-day birth season for P. v. verreauxi at Berenty, in the south of the island. In neither case was the distribution of births through time sufficient to indicate a polyoestrus breeding system.

In 1965, Lancaster and Lee surveyed the research that had been done on the ultimate and proximate factors determining the periodicity of primate reproductive cycles, and pointed out the need for further work in this field. The effect of the photo-period on Microcebus has been demonstrated by Petter-Rousseaux (1969). The breeding season of L. catta shifts by six months when animals are brought to Europe (Martin, pers. comm.). However, controlled experiments have yet to be done on both L. catta and P. verreauxi to establish the precise influence of day length and of temperature on sexual behaviour in these species. Since L. catta is polyoestrus in captivity and not in the wild, it is likely that, in this species at least, proximate ecological factors which repress

and then induce oestrus are operative in the wild. The absence of these factors in captivity would permit the appearance of a full polyoestrus system. The effect of general physical condition on females' ability to come into oestrus is not well understood; seasonal fluctuations in food availability in the two study areas are discussed in detail in Section V, but, in summary, food seems to be scarce at the end of the dry season, particularly in the south where the rain starts after a six month drought. Food availability increases to a peak towards the end of the wet season in March, and then drops off again in the dry season. It is to be supposed that the physical condition of the animals mirrors this pattern to some extent and that full oestrus, if affected by the female's physical condition, would be most likely to occur towards the end of a period of optimal ecological conditions, in this case March. It is immediately apparent, however, that other phases, such as pregnancy, suckling infants, or weaning infants, may be more critical and that the system is timed to provide optimum conditions during one of these periods. In ultimate terms, the periodicity and control of the cycle are likely to be closely adapted to the environment in such a way as to ensure the maximum survival of populations. The timing observed in this study was as follows: mating occurred at the end of the wet season, gestation from the end of the wet season through the first half of the dry season, births in the middle of the dry season, suckling until the end of the dry season, and then the infants are almost completely weaned at the beginning of the following wet season.

The similarity between L. catta and P. verreauxi, postulated above from limited evidence, is substantiated in other aspects of their mating systems: the receptivity of Group IV females FNI and FI lasted a

maximum of 42 and 36 hours respectively, as compared with a maximum of 36 hours for L. catta in the wild (Jolly, 1966) and 10 - 24 hours in captivity (Evans and Goy, 1968). The incidence of marking behaviour by females in this study was not affected by the breeding season, and a similar stability is reported in L. catta females in captivity (Evans and Goy, 1968). Finally, Evans and Goy report that "both long and short term fluctuations in gonadal activity were associated with changes in the frequency of expression of several non-sexual patterns," although they do not differentiate clearly between "sexual" and "non-sexual" patterns. In P. verreauxi it has been shown that changes in the frequency of five activity patterns occurred in the pre-copulatory period and that, as in L. catta, only two new patterns appeared: the act of copulation itself, and fierce fighting between adult males. It is probable that these frequency changes were associated with changes in gonadal activity in P. verreauxi in this study.

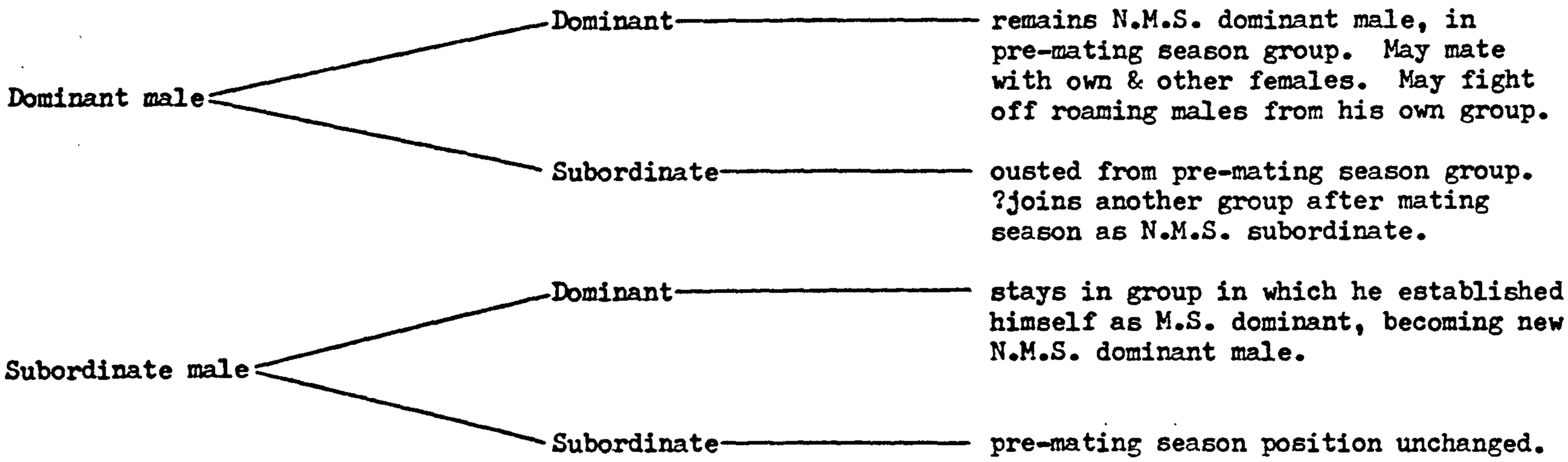
The close relationship between Groups III and IV has already been referred to. The basis of this relationship is not understood. Interactions are frequent but never friendly and it is unlikely that Groups III and IV had recently split up from one larger group since, in September 1970, Group IV seemed to be in the process of splitting away from a group to the south of its range (in prep.). The presence of three unknown animals sunning themselves in the same tree as Group IV, in the south of their range in mid-February, suggests that the split was not complete even by then. It is postulated that the frequent encounters between Groups III and IV led to an across-group recognition of individuals although not to a stable dominance hierarchy between the two groups considered as whole units. It is further suggested that $\vec{O}$R(IV) recognized $\vec{O}$F(III) as a dominant male. This contrasts with his reaction to $\vec{O}$P, a subordinate male in Group III: $\vec{O}$R(IV) fought $\vec{O}$P(III) for 24 hours to

prevent him approaching either adult female in Group IV.

In the light of the circumstantial evidence, it seems improbable that events described in Group IV were atypical. Milne-Edwards and Grandidier (1876) refer to fighting "pendant la saison des amours." There are many anecdotal accounts of fierce fighting in February and March, and a reliable first-hand account of one such fight was given to Jolly (1966) by S. de Guiteaud. Further, the adult males in all four study groups had torn ears and old facial scars. Since only one female had a slightly torn ear it is more likely that the males acquired these scars through fighting than through falling.

Given the various interpretations possible, the following tentative hypothesis is put forward as one explanation of the differential reaction observed of females towards males, and males towards each other. It should be re-emphasized that this hypothesis refers only to the sub-species P. v. verreauxi. The crux of this hypothesis is that priority of access to females, food and space, during the mating season, i.e., "mating season dominance," is not necessarily a correlate of priority of access to food and space before the mating season, i.e., "non-mating season dominance." During the breeding season "roaming" behaviour by adult males occurs at the same time as some degree of break-down in group structuring; this break-down is marked by the appearance of aggressio directed at previously dominant males by previously subordinate males. This aggression may occur with respect to access to food, resting places, or females. As in L. catta (Jolly, 1966), frequency of mating - although not demonstrably of fertilization - is not the prerogative of N.M.S. (non-mating season) dominant males. This does not mean that dominance becomes a meaningless concept during the mating season but that the actual structure of the N.M.S. feeding hierarchy changes at the onset of

Figure 41: Possible changes in adult male status as a result of the mating season.



this period: P. verreauxi females allow only males dominant in the immediate situation, that is males dominant in the mating season (M.S.) to mount them. This M.S. dominance may be established through previous mutual knowledge and be an extension of N.M.S. dominance. However, M.S. dominance can also be achieved by previously N.M.S. subordinate males, through fighting and ousting N.M.S. dominant males. Unlike L. catta, where there is a total reversion to the previous N.M.S. hierarchy at the end of the mating season (Jolly, 1966), the assertion of M.S. dominance in P. verreauxi appears to have enduring effects on the structure of N.M.S. dominance within a group. A male dominant both in and out of the mating season mates with females in one or more other groups but remains a member of the group in which he was dominant before the mating season. The N.M.S. subordinate male who has fought his way to M.S. dominance in a group by ousting the resident N.M.S. dominant male, may stay in that group, be it his own original group or one encountered while roaming, to become N.M.S. dominant after the mating season. Figure 44 illustrates this idea further.

With reference to ♂P(III), it is suggested that he returned to Group III only because he in turn was ousted from Group IV by ♂INT. Under the interpretation above, ♂R(IV) recognized ♂F(III) as dominant both in and out of the mating season and hence as no threat to his own position of non-sexual dominance in Group IV; in contrast, ♂P(III), a non-sexual subordinate, did constitute a challenge to ♂R(IV)'s position and fighting resulted.

It is not known whether ♂F(III) mated with adult females FD(III) and NFD(III) or whether a roaming, M.S. and N.M.S. dominant male did so. It is certain that ♀FI(IV) and ♀FNI(IV) refused to mate with ♂R(IV), even when they were receptive and prepared to mate with roaming males. According

to the interpretation above, this was because the non-sexually dominant male, R, was being successfully challenged by intruders - $\vec{\sigma}$F(III), $\vec{\sigma}$P(III) and $\vec{\sigma}$INT.

Finally, some consideration should be given to the selective advantage of the system. The evidence indicates that the system ensures some degree of outbreeding. Although this outbreeding is probably limited to neighbourhoods, it would be likely to produce some gene flow through the population as a whole. This might be important in a species with a group size of less than 10, where chronic in-breeding might otherwise occur. New males did join Group I in the north outside the mating season, however, with no apparent fighting involved; it seems unlikely that the mating system, with its fierce inter-male fights, evolved simply to counter in-breeding, when more peaceful means of changing group were possible outside the mating season.

The system might also operate to produce intra-sexual selection between adult males. Access to females and, by inference, biological paternity, appears to be dependent upon the fighting ability, strength and endurance of the adult male. This may have been proved in the previous year, or years, or may only be manifested in the current mating season. Fighting ability, strength and endurance cannot be equated with overall fitness; however, it does seem unlikely that there should be intensive selection for fighting prowess specifically, during the mating season, when no fights were witnessed during the rest of the year. An alternative explanation is that the social upheaval and fights of the mating season do to some extent test the fitness of the males in terms of their ability to survive relatively prolonged periods of high energy output without a concommitantly increased energy input. This might be critical in a species subject to fluctuations in food availability.

Finally, within the framework of the whole social system, the mating

system should be seen not as a cohesive social force but as a catalyst: although animals did join and leave groups at other times without a great upheaval, the mating season par excellence seemed to permit an extensive break-down and reshuffle in an otherwise fairly rigid social structure. This structure was oriented towards access to food rather than to females, and when access to females came into question, the structure apparently became largely irrelevant but reappeared, modified, after the mating season. Thus the mating system can be seen as an integral part of a dynamic social process, as an important counter to the isolated, rigidly structured small-group system of the rest of the year, and as further evidence of yet another species where the pair bond is not the overriding cohesive factor in group relationships.

SUMMARY

1) In this Section, observations recorded during the mating season in the south are described.

2) Flushing of one adult female's vulva in Group IV in mid-January coincided with a sudden, significant increase in the following activities: "endorsing" by adult males, "sniff-approach and marking" by adult males, "roaming behaviour" in adult males, intra-group agonistic encounters, and inter-group encounters. Comparable changes were not observed in Group III.

3) Copulation was said to have occurred when ejaculation took place. Copulation by three males with the two females in Group IV was observed between March 3rd and 6th. This was the only period during the field study when male/male and male/female mounting was observed. Males mounted females as they clung to vertical trunks. The frequency of the activity patterns listed in (2) reached a peak during the four days when copulation occurred. It should be noted that although copulation

was never seen in Group III, the two adult females did produce infants in the following August.

4) Typically, during the copulatory period, one or other female acted as a focus for male attention, yet rejected the majority of male advances, and there was persistent inter-male aggression.

5) ♂F, from Group III, copulated with ♀FI(IV) with relatively little interference from other animals. ♂P(III), however, fought ♂R(IV) for 24 hours before he finally ousted the latter from Group IV. ♂P then copulated with ♀FI, but was himself ousted by another intruding male, ♂INT. ♂INT copulated with ♀FNI, and stayed with Group IV until the end of the study. ♂P returned to Group III and resumed his subordinate position.

6) The data suggest that P. verreauxi have only one full oestrus period in the breeding season, but that there was a period one month earlier analagous to the "pseudo-oestrus" period described in L. catta (Jolly, 1966).

7) It is postulated that the frequent encounters between Groups III and IV led to an across-group recognition of individuals, although not to a stable dominance hierarchy between the two groups considered as whole units.

8) In the light of the circumstantial evidence, it seems improbable that events described in Group IV were atypical.

9) During the mating season there was some degree of break-down in group structuring: this was marked by the appearance of aggression directed at males with a high rank in the feeding hierarchy by males ranking low in that hierarchy. It is postulated that a male dominant both in and out of the mating season mates with females in one or more other groups but remains a member of the group in which he was dominant before the mating season. The non-mating season subordinate male who

has fought his way to mating season dominance in a group by ousting the resident non-mating season dominant male, may stay in that group, be it his own original group or one encountered while roaming, to become non-mating season dominant male after the mating season.

10) The system ensures some degree of out-breeding. It also apparently operates to produce intra-sexual selection between adult males. It is possible that the social upheaval and fights of the mating season to some extent test the fitness of the males in terms of their ability to survive relatively prolonged periods of high energy output without a concommitantly increased energy input. This might be critical in a species subject to fluctuations in food availability.

11) The mating system should be seen not as a cohesive social force but as a catalyst, permitting an extensive break-down and reshuffle in an otherwise fairly rigid social structure. This structure was oriented towards access to food rather than to females, and when access to females came into question, the structure apparently became largely irrelevant but reappeared, modified, after the mating season.

Plate 11. Adult male in posture (f) - lying along horizontal support.

Plate 12. Adult female in posture (h) - "sloth" position.

Plate 13. Bark stripped from tree trunk by P.v. coquereli while feeding.

Plate 14. Adult female in typical "sunning" posture.

Plate 15. Animal in the middle of a leap between two vertical supports.

Plate 16. Adult male making submissive gestures: tail rolled up between legs, back hunched, bared teeth.

Plate 17. Sub-adult male grooming adult female's head.

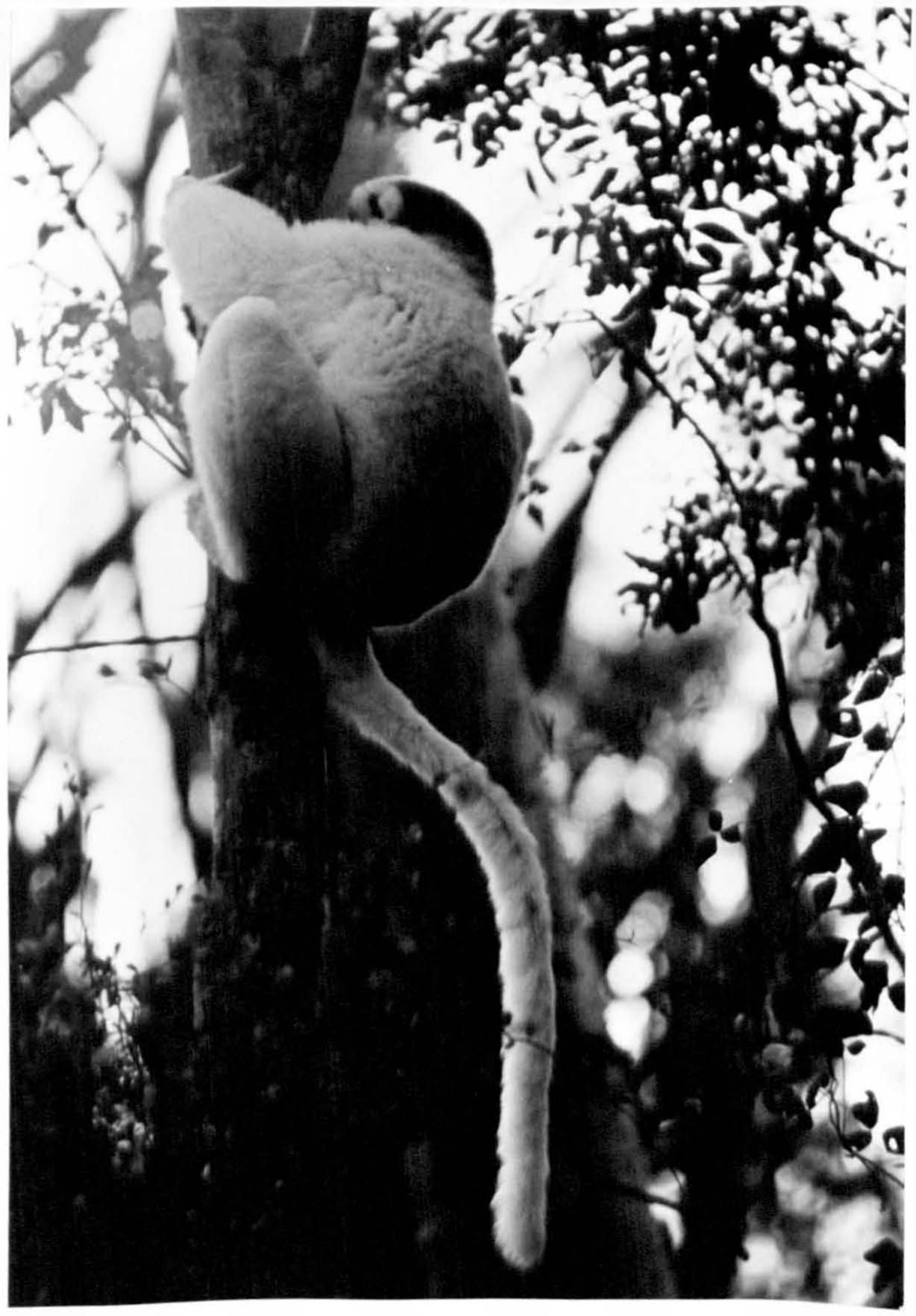
Plate 18. Two animals play-wrestling.

Plate 19. Adult female lying on her back on ground during a play bout.

Plate 20. Adult male sent-marking with throat gland.

Plate 21. Adult male scent-marking with perineal area.

Plate 22. Adult ♂ P, showing his disfigured nose after the mating season.



PART III:

DISCUSSION

PART III: DISCUSSION

The aims of this study were closely related. Detailed comparative data were collected on a prosimian species, Propithecus verreauxi, in order to provide a broader overview of the whole range of primate behavioural adaptations. The study was conducted in two, ecologically contrasting areas to permit an investigation of the flexibility of social organization of P. verreauxi. In using this comparative approach, an attempt was made to identify and understand some of the processes by which ecology may influence social organization.

The ranging and feeding patterns, daily activity patterns and social structure of the study groups were considered separately, and compared and contrasted between and within study areas. An analysis of the structure and composition of the habitat in each study area was also made.

Here, an attempt is made to provide an integrated assessment of the extent to which the aims of the study were realised. A general picture of the social organization and ecology of P. verreauxi is given and placed in a context of the total variation found among known primate societies. The degree of behavioural divergence between the groups in each area is considered, and the spectrum of factors that may determine these differences is discussed. Finally, consideration is given to the comparative significance of the results, and the methods used, for primate studies.

The distribution, social organization and ecology of primates

Primates are found living terrestrially in open savannah as well as living totally arboreally at all levels of the forest, but their distribution is generally limited today to tropical and sub-tropical zones of the

world. Man provides a striking exception to this generalization, and so to a lesser extent does the Japanese macaque. This species is found in mountainous areas of Japan that are snow-covered during three months of the year (Yamada, 1966). It is also probable that, in the past, species extinct today were distributed through temperate regions (Simons, 1972).

During the past thirty years, a considerable body of data has been collected on the social organization of a limited number of primate species, although perhaps two-thirds of the total number of extant species have still to be studied in depth. However, despite the fact that relatively few species have been studied and that non-human primates have a limited world distribution, it is already apparent that within the Order there is extensive variation in social organization. Attempts have been made to establish systems of classification based on currently available information (e.g., Crook and Gartlan, 1966; Eisenberg et al., 1972). These classifications have a number of shortcomings, not the least of which is that they frequently lump together what are in reality highly diverse types of social organization, and thus underestimate the real variability that exists amongst primates. However, with this understanding that present classifications minimize rather than accurately reflect diversity, they can provide useful indicators of the spectrum of variation known to exist.

The social organization of primates falls into at least four main types, or categories. The first, that of "solitary living" animals, is characteristic of most of the nocturnal prosimians. Animals in this category generally move and feed alone, each having its own home-range. However, field studies indicate that this solitude is more apparent than real (Charles-Dominique, 1972; Martin, 1972): contact between animals is maintained through olfactory communication and vocalizations. Males

"visit" oestrus females and, in the case of Microcebus murinus, females share their nests not only with their immature off-spring but also with other adult females. Less commonly, males may sleep in pairs (Martin, 1972). Recent research has shown that the orang-utan, Pongo pygmaeus, may also share a similar pattern of social organization (McKinnon, pers. comm., Rodman, pers. comm.).

The second general category, that of "family living" groups, is exemplified by the gibbon, Hylobates lar, and one of the little studied New World monkeys, Callicebus molloch. These species live in stable groups consisting of an adult male, an adult female and their immature off-spring. As the off-spring mature, they leave, or are driven, from the group and form new pair-bond groups with young animals from other groups (Ellefson, 1968; Mason, 1968).

"One-male" groups form the third category. In this pattern of social organization, groups comprise one adult male and a number of females and their off-spring. Three savannah-living species, Erythrocebus patas, Papio hamadryas, and Theropithecus gelada, are known to live in groups of this type (Hall, 1965b; Kummer and Kurt, 1963; Crook, 1966). A number of forest-living Cercopithecoidea are also reported to live in one-male groups (Struhsaker, 1969b).

The fourth category is that of "multi-male" groups. These groups are composed of a number of males and females and their off-spring, living together without stable heterosexual bonds being apparent. This type of social organization is common to all the macaques, many baboon species and most of the South American monkeys that have so far been studied (Kummer, 1971).

No simple relationship exists between the variation observed in social organization and ecology among primates. The interplay between these

factors is complex, and species living in the same habitat may exhibit different patterns of social organization and, related to this, different patterns of exploitation of their environment, while species living in highly contrasting habitats may exhibit apparently similar patterns. A comparison of five species, all of them forest-living and two of them actually studied in the same forest, illustrates this point. Hylobates lar is found in tropical rain forest in South East Asia. This species lives in family groups occupying about 1km^2 of the forest. Each group has its own exclusive range which it defends against intrusions by neighbouring groups (Ellefson, 1968). In contrast, Miopithecus talapoin lives in groups of 60-80 animals, in the rain forests of West Africa. These groups have a range of 4-5km^2, and overlap between the ranges of adjacent groups is minimal or non-existent. However, no evidence has been found to indicate that groups actively defend these exclusive ranges: exclusivity seems rather to be maintained by avoidance (Gautier-Hion, 1966). Further contrast is found in Colobus badius and Colobus guereza. These species are found living sympatrically in mixed deciduous and tropical rain forest in East and Central Africa. Like the talapoin monkey, C. badius may live in groups containing over 80 animals (Struhsaker, pers. comm.), moving in an area of 0.3-0.5 miles^2; however, in this species home-ranges do not overlap. When groups encounter each other, the interaction may consist merely of reciprocal staring or may involve more active agonistic behaviour. C. guereza lives in groups of only 8-12 animals, usually containing only one adult male (Oates, pers. comm.). These groups range over an area of about 0.1 miles^2. These ranges are actively defended, although spacing between groups is probably also maintained through a system of vocalizations. Finally, Pan paniscus in Tanzania lives in "groups" of about 40 animals, which range over an area of about 15 miles^2. However, much of the time these "groups" are dispersed in

small foraging parties containing only a few animals; the composition of these foraging parties may change through time, and the whole "group" generally assembles only at the site of a particularly large and abundant food resource (Suzuki, 1969).

In summary, it is clear that just as different "ecological problems" may be solved through apparently similar patterns of group dispersion and social organization by different species, so may the same "ecological problem" be solved in different ways by different species. It should further be noted that the examples quoted above are taken from studies made on a small sample from a population living in a specific locality: it is possible that further fieldwork may show extensive variation within these species as well as between them.

Propithecus verreauxi: social organization and behavioural variation

Propithecus verreauxi is found in the remaining deciduous forests of north, west and south Madagascar, and also in the arid Didierea forest that covers extensive areas of the south. In this study, two groups were watched in mixed deciduous forest in the north-west of the island, and two groups in Didierea forest in the south. The behavioural variation found was of three kinds: there were regional variations between the groups studied in each area; variation between seasons was observed in the behaviour of each group; thirdly, there was local variation, or variation between groups living in the same forest.

The behavioural variation between seasons within a given group was generally found to be greater than that between any two groups at a given time. However, there was one important exception to this: a striking difference existed in the pattern of group dispersion between the two regions.

In the following discussion, aspects of the social organization and behaviour of the four groups studied are considered, and the relative importance of regional, seasonal and local variation assessed.

Group size and composition. Groups were counted ranging from 3-10 in size, although groups of up to 13 have been reported (Sussman, pers. comm.). No significant regional variation in group size was found, although surveys were made in five separate localities. Although the overall sex ratio for all groups censused was approximately unity, the sexual composition of individual groups varied to such an extent that no norm of group composition could be established. Thus groups could be found fitting the description "one-male group," family group," and multi-male group." In this species the group should be viewed as a foraging party of mutually familiar animals rather than as a reproductive unit of predictable composition.

It is of interest that the evidence from Berenty no longer indicates an excess of males: in censuses in 1963/1964, Jolly found a significant imbalance of males. The results of censuses in 1970 (Jolly, 1972) and 1971 (this study) show that the sex ratio is now approaching 1:1. Reasons for the previous imbalance can only be speculative: it is possible that a disease differentially affecting females reduced the number of females in groups at that time, or that there was a higher rate of immigration into the reserve by males than be females. Some support for the latter theory is given by the fact that males may leave their groups and join new groups both in and out of the mating season. In contrast, no female was seen to change groups in the course of the study. This pattern of female stability and male mobility is in keeping with the evidence from many primate societies (see Rowell, 1973; Altmann and Altmann, 1970; Lindburg, 1967).

Patterns of group dispersion. There was no significant difference in home-range size between groups living in the two study areas: all groups moved in an area of 8-9ha. However, in the south each group had exclusive use of a much larger proportion of its home-range than in the north. This area of exclusive use, or "monopolized zone," comprised a large block of forest in the centre of each group's home-range in the south; inter-group encounters only took place in the narrow zone of overlap around the periphery of the central monopolized zone. In contrast, areas of exclusive use within the home-ranges of the northern groups were scattered and may even have been an artifact of the observational techniques employed. Inter-group encounters occurred throughout the extensive areas of overlap with other groups. Although inter-group encounters in the north were more common, the characteristic inter-group "battles" described by Jolly (1966) occurred proportionately more frequently in the south. In the north, encounters appeared to be more in the nature of avoidance actions than confrontations: frequently, groups approached each other, stared and then moved apart. More active "battles" did occasionally occur, but they did not appear to delimit geographical area as they did in the south, and usually they took place with reference to a preferred food source at which one of the groups was feeding at the beginning of the encounter.

In summary, dispersion in the north generally occurred through visual awareness followed by mutual avoidance by groups, and was associated with extensive home-range overlap, whereas in the south it was probably achieved through the maintenance of a defended territory by each group. Thus, the overall pattern of exploitation of the environment was not a consistent, species-specific characteristic but rather varied regionally.

Ecological variation that may be related to this regional difference is discussed below (P. 337). However, even if ecological parameters that

affect behaviour can be identified, the biological basis of the behavioural variation remains obscure. It is possible that the observed variation was simply a manifestation of a species-specific capacity for behavioural flexibility. It is also possible, however, that the different, and presumably adaptive, responses exhibited by groups in each study area reflected genetically determined, inherited differences characteristic of each sub-species.

Viewed comparatively, the northern study groups' pattern of dispersion showed similarities to that of Alouatta palliata (=villosa, Richard, 1970) in that they both have overlapping home-ranges and a low level of overt inter-group aggression. However, the latter species maintains inter-group spacing chiefly through a system of vocalizations, and less commonly through visual awareness followed by avoidance or a more patently hostile interaction. The speciousness of simplistic, across-species comparisons of this nature is clear, however, when parallels are sought for the pattern of dispersion of the southern groups: the two primate species known to live in small groups, in relatively small, defended ranges are Callicebus molloch and Hylobates lar. However, both these species occupy dense tropical rain forest; it would to us seem to serve little purpose to classify the Didierea forest-dwelling P. v. verreauxi with these species. Although it is interesting to find three, very distantly related, primate species exploiting at least two radically different environments using similar patterns of dispersion, it is improbable that these patterns evolved in response to similar ecological pressures or that the similarity is more than superficial. Ellefson (1968) indicated that in the case of H. lar each group defended an area containing a few, highly critical food trees upon which animals relied heavily and regularly for their food. In contrast, it is likely that groups of P. v. verreauxi defended a range containing very many small, scattered food sources all of which were of

critical importance at certain periods of the year.

Ranging and home-range utilization. Although the study groups each ranged over an area of 8-9ha., 2-3ha. of this area were used less than 5% of the time by the group. Further, a few parts of the home-range were used much more heavily than others by the group, although the extent to which each group showed this tendency towards intensive use of particular parts varied. The variation was group-dependent rather than region-dependent, however. These areas of intensive use were not necessarily clumped together and hence were called "foci of activity" rather than a "core area." Amount of use was not related to exclusivity of use; a corollary of this was that in neither study area were foci of activity necessarily areas of exclusive use. No differentiation could be made between parts of the home-range, including the foci of activity, according to the type of activity performed in them.

All four groups visited most parts of their home-range within ten to twenty days, but although several general patterns of daily movement recurred, no evidence of a regular cycle of movement around the range was found. There was an overall difference in the mean daily distance moved between the northern and southern groups: the northern groups consistently moved further each day than the southern groups. There was also significant, within-group seasonal variation in daily distance moved: in the wet season groups sometimes moved more than twice as far in a day as they did during the dry season. Related to this increase in day ranges during the wet season, there was also a slight increase in the number of different grid squares entered, and a larger increase in the total number of squares entered during each six-day observation block. This indicates that in the dry season groups tended to spend more time in a smaller area of their home-range. However, although in the wet season animals tended

to spread their time more evenly over a larger area of the home-range, the result was not an appreciable expansion of home-range size but rather a shorter time-span within which the whole home-range was visited at least once.

Diet and feeding behaviour. The general characteristics of feeding behaviour were similar in both study areas. Animals adopted many feeding postures, enabling them to feed in most parts of any tree. In the wet season, all four groups tended to have two feeding bouts, one in the morning and one in the afternoon; in the dry season, there was one main feeding bout which reached a peak towards midday. Further, animals in the south fed for much shorter periods each day in the dry season than in the wet season. This difference was also seen to a less striking degree in the north.

Regional, seasonal and local variation was found in the diet of P. verreauxi. Considering first regional variations, the species composition of the groups' diet was almost completely different in each study area. This was largely, but not uniquely, due to differences in the vegetational composition of the two forests. Four tree species were identified which were common to both forests. One of these was eaten commonly by both northern groups, but in the south neither group spent more than 1% of total feeding time eating it. The second species was eaten in quantity by the southern groups, but rarely in the north. Further, in the south animals ate only the green and ripe fruit of this species, whereas the northern groups ate only its flowers. The third species was eaten commonly in the south, but no animal was ever seen eating it in the north. The fourth was eaten commonly in the north, but was never touched by animals in the south. A number of explanations for this difference are possible: environmental factors such as soil type may have modified the

nutritional value of these species in each region, making them important dietary components in the one and not in the other. In cases where a species was eaten in one area and not in the second, it is possible that other species may have been preferred alternatives, providing equal, or greater nutritional value. Finally, this variation may have had no nutritional basis but be rooted in regional traditions of food preference.

The diet of the southern groups contained fewer species than that of the northern groups. This does not, however, mean that the southern groups were more selective in their choice of foods: fewer tree species were present in the southern forest, and animals in fact fed on a proportionately wider range of the species that were available than did the animals in the north. It could thus be said that the southern groups were proportionately less selective, and in this way they maximized the diversity of their diet. Associated with this absolute difference in total diversity, the two southern groups spent a greater percentage of the total feeding time eating relatively few food species than did the northern groups.

Within each study area, a number of changes occurred seasonally. The direction of these changes was similar in both study areas, although the change was generally more pronounced in the south. There was an almost complete change in the species composition of the diet of all four groups between seasons, as well as a significant change in the food part being eaten. In the dry season, animals fed chiefly on adult leaves and dormant buds; in contrast, their diet in the wet season contained a high proportion of young leaves, flowers and fruit. It is also interesting to note that, in the south, although animals were never seen eating dead wood, in the dry season the bark and cambium of Operculicarya decaryi constituted an important component of their diet. This contained a high percentage by weight of water and may have been critical for survival during the

arid dry season. In the north, animals ate bark to the exclusion of dead wood during the dry season, and dead wood almost to the exclusion of bark during the wet season. No evidence of the presence of insect life was visible to the human eye in this dead wood, and its significance for the diet of P. v. coquereli is not understood.

In addition to these seasonal differences in the species composition of the animals' diet and in the type of food being eaten, there was also a marked seasonal change in the diversity of diet of the two southern groups: both groups fed for longer periods on fewer species in the wet season and the overall diversity of their diet was reduced. There was no overall reduction in the diversity of the northern groups' diet, but if only those foods on which each group spent more than 1% of total feeding time are considered, a seasonal effect can be seen: animals spent more time feeding on fewer species in the wet season than in the dry.

Local variation, or variation between the two groups within each study area, was found in the species composition of their diet. In both the north and the south, only eight of the twelve species most commonly eaten by each group in that area were the same. This may have been due to "cultural" differences between the groups or to local differences in the availability and distribution of the various food species.

Daily activity patterns. In both study areas, the pattern of feeding, moving and resting was similar, and the nature of the changes in this pattern between seasons was also comparable. In the dry season, animals often did not move until an hour or two after sunrise, at which point they would take up stations high in the trees, exposed to the sun. This "sunning" activity might last for over an hour before the group finally moved off to feed. Animals fed more or less continuously until early afternoon, when they moved into the forks of trees and took up their

sleeping positions, in which they would remain until the following morning. The pattern in the wet season provided a striking contrast: animals were usually moving about and feeding before sunrise, and most feeding activity ceased by mid-morning. Animals then slept until the middle of the afternoon before resuming their feeding and foraging activities until after sunset. In both study areas, more time was spent in the shade during the wet season than during the cooler dry season.

Animals rarely travelled long distances in one concerted movement: only when fleeing from dogs or man did they move more than about 50m. without pausing. Although many postures were assumed while feeding, when travelling animals habitually used a "vertical clinging and leaping" mode of locomotion. In neither study area did they spend much time on the ground, but all other types of substrate were used extensively. The similarity of the results for posture and substrate use in each study area contrasts with the considerable differences apparent between the physical structure of the two forests. It is thus possible that animals were highly selective in their choice of substrate so that the differing physical parameters of the forests had little influence on the frequency with which different postures or modes of locomotion were employed.

Social structure and mating season. In all groups, most agonistic encounters outside the mating season occurred in a feeding situation, although aggression was also commonly seen when animals tried to handle a mother's infant: the mother would cuff and bite to prevent them gaining access to her infant. Using priority of access to food as the criterion of social dominance, a clear-cut hierarchy was evident: aggression in this context was unidirectional, and the outcome of agonistic encounters could be predicted with a high degree of accuracy. However, this hierarchy was referred to only as the "feeding hierarchy" because there

was no consistent correlation between the rank of individuals ordered according to the criterion of priority of access to food and their ranks in hierarchies established according to the frequency of aggression, the direction and frequency of grooming, or preferential access to females. Although the highest ranking animal in the three groups whose social structure was studied in depth was a female, dominance in the feeding hierarchy was not necessarily a function of sex: in one group, an adult male always had priority of access over an adult female.

The presence of infants and the associated rise in their mothers' frequency of aggression probably played an important part in regulating social structure within the group. Further, there was limited evidence of what may be called idiosyncratic relationships between animals and of changing relationships between sub-adult and juvenile animals. All these factors tended to increase the complexity of relationships within each group, so that it would be an oversimplification to see the social structure of P. verreauxi in terms of a unitary theory of social dominance manifested in a simple, pervasive hierarchy.

The frequency of agonistic behaviour varied from individual to individual and from group to group, but no consistent variation was found between regions. However, in all four groups agonistic encounters occurred more frequently in the wet season than in the dry. Most animals contributed to this overall increase, and in no case was a decrease in frequency recorded. The increase during the wet season may have been due to the fact that animals were generally more active and feeding for longer periods: since most aggression occurred in a feeding situation, an increase would be expected when animals were feeding more. It is also probable that the advent of the mating season resulted in further heightening of frequencies of aggression in the south.

Allo-grooming was the most commonly observed non-agonistic interaction. Adult females generally initiated less grooming and were more commonly groomed than other group members. Associated with this observation, there was a tendency for animals dominant in the feeding hierarchy to groom least and be groomed most, those subordinate in the hierarchy grooming most and being groomed least. However, the existence of frequent grooming as a function both of maternity and of harrassment of one animal by another complicated relationships and removed the simple linearity of the feeding hierarchy.

Copulation by three males with the two females in Group IV was observed between March 3rd and 6th. This was the only time during the field study when male/male and male/female mounting was observed. Neither of the females in Group III was seen to copulate, although they both produced infants the following August.

A number of behavioural changes were noted during the copulatory period: typically, one or the other female acted as a focus for male attention, yet rejected the majority of male advances. Associated with this, there were significant increases in marking behaviour and "roaming" by adult males. Further, both intra- and inter-group aggression was more frequent. It should again be noted that these changes were not observed in Group III, although mating must have taken place.

The increase in intra-group aggression was accompanied by some degree of breakdown in group structuring: previously subordinate animals, particularly males, began initiating aggression against dominant animals, thus removing the unidirectionality of the feeding hierarchy.

The sample size was small, and the data available on that sample limited so that attempts to explain the intense and unusual activities of the mating season must be speculative. It is postulated that a male dominant in the feeding hierarchy both before and during the mating season mates

with females in his own and/or one or more other groups, but remains a member of the group in which he was dominant before the mating season, and retains his status in that group. A male subordinate in the feeding hierarchy prior to the mating season may fight his way to gain access to oestrus females by ousting the resident feeding-hierarchy dominant male in his own or another group. After the mating season, this previously subordinate male may stay in the group from which he ousted the dominant male and become the dominant male in the feeding hierarchy himself.

This pattern of mating ensures some degree of outbreeding: it seems that males often mate with the females from other groups. It also apparently operates to produce intra-sexual selection between adult males. It is possible that the social upheaval and fights of the mating season test the fitness of the males in terms of their ability to survive relatively long periods of high energy output. As an integral part of the social structure, the mating season should be viewed not as a cohesive social force but as a catalyst, permitting an extensive break-down and reshuffle in what are otherwise small, fairly isolated units.

I was not present during the mating season in the north, so no data are available for a regional comparison. It is emphasized, therefore, that the pattern described above should not be considered characteristic of the whole species.

From this survey of various aspects of what is here loosely termed the "social organization" of P. verreauxi, perhaps the most important feature which emerges is the extensive variability of this animal. Although the variation found was not as striking as that reported in, for example, the langur (Yoshiba, 1968), it is nonetheless clear that an accurate picture of the behavioural capabilities of P. verreauxi cannot be reflected by a brief study of any one group living in one particular forest. Within

broadly defined limits, a general pattern did exist, but within these limits the variation was such as to suggest that in at least this prosimian species behavioural adaptability was not significantly less than that reported for many of the Anthropoidea.

Ecological correlates of behavioural variation in P. verreauxi

A comparison was made between the same groups in different seasons, and between populations of the same species, P. verreauxi, living in different habitat types. Data were collected on the two aspects of ecological variation that appeared to be important with regard to the populations studied, namely climate and vegetation. Certain correlations emerged between the observed behavioural and ecological variation. These are considered below. However, although such correlations may signify causal relationships, this can be neither assumed nor demonstrated in the present study.

Other parameters in addition to climate and vegetation may have played a critical role in determining the social organization of P. verreauxi. Chivers (1969), for example, has suggested that changes in the population density of howler monkeys on Barro Colorado Island is leading to changes in social organization. In that instance, however, it is difficult to determine whether the density factor is operating directly or through its effect on food resources. Mittermeier (pers. comm.) has suggested that the heaviness of rainfall has a profound effect on the ranging and feeding patterns of these same animals. Again, the influence of predation pressures on social structure has been discussed extensively (e.g., Crook and Gartlan, 1966). While the paucity of data concerning predation on P. verreauxi suggests that the influence of predators is minimal, this inference may be misleading. It is possible, if unlikely,

that differential pressures due to predation were operative in the two habitats, or that the social organization seen today was formed at a time in the past when predation was a much more critical factor than it is today.

While some of the behavioural variation seen may have been associated with parameters of which no account was taken in this study, I believe that some if it, particularly the "local" variation, was random and of no adaptive significance. For example, while ecological factors may determine the upper limit of group size and may favour social rather than "solitary" living, within these limits group size and sex composition may be arbitrary. Similarly, local differences in the species composition of diet, and in the amount of time spent feeding on particular foods, may reflect arbitrary differences of "tradition" between groups rather than a real difference in food availability.

Temperature and Daylength. It is likely that exposure to extremes of high and low temperature has favoured the development of behaviour patterns in P. verreauxi that help maintain a constant body temperature. These patterns include "sunning" behaviour, huddling together at night, and a tendency to spend more time exposed to direct sunlight during the cooler dry season.

Although no controlled experiments have yet been carried out on the physiology and, specifically, thermo-regulation of P. verreauxi, Bourliere et al. (1953, 1956) have investigated the relation of rectal temperature to fluctuations in ambient temperature in some of the smaller prosimians. They found that animals in captivity exposed to wide temperature fluctuations did not maintain a constant body temperature. Rainey's (1970) work on the rock hyrax showed that this mammal is unable to maintain its body temperature at a constant level by physiological mechanisms

alone: behavioural responses to changes in ambient temperature are also critical. I believe that, similarly, the behavioural responses of P. verreauxi are critical for thermo-regulation, but until controlled experiments are performed on animals able to bring to bear both physiological and behavioural responses, and on animals only able to make a physiological response, to ambient temperature variations, the importance of behavioural regulation remains open to speculation.

It is possible that the change in activity pattern during the dry season was partly attributable to the drop in nighttime temperatures at that time: animals became active only when the ambient temperature had risen several degrees from its dawn level and they had sat in the sunshine for an hour or more. Even unhabituated animals were sluggish at the time and rarely moved off or responded strongly to my presence immediately, although they always did so at other times of day. This late start to the day's activities in the dry season may have been due to animals' need to raise their body temperature after being exposed to the relatively low nighttime temperatures. Using the sun as an energy source would seem the most efficient way of doing this. It is also possible that the increased energy output required for thermoregulation in the dry season, due to exposure to geater extremes of temperature, may have reduced the amount of energy available for other activities, and thereby contributed to the overall reduction in activity and, particularly, the cessation of all play behaviour, during the dry season.

However, Stoltz and Saayman (1970) have shown that the daily distance covered by the chacma baboon in the northern Transvaal is inversely related to maximum daily temperature: animals tend to move further on cooler days. No season effect was found, but nor was there a significant seasonal difference in maximum daily temperatures. Clutton-Brock (1972) reported that a group of C. badius ranged further each day during the cool dry season

than it did during the warmer wet season. Thus caution should be exercised in inferring causal relationships from simple correlations observed between temperature and activity levels. It is very likely that in P. verreauxi factors such as the distribution and availability of food were also important in determining daily patterns of activity and the length of day ranges. On the available evidence, the relative importance of temperature and these other factors cannot be determined.

In both study areas, day length varied between seasons by about three hours. This may have contributed to seasonal variation in activity patterns. Pariente (in press) has shown that light levels provide critical triggering mechanisms in the activity cycle of Lepilemur mustelinus. However, P. verreauxi was usually moving and feeding in the halflight before sunrise in the wet season, and continued to feed in the evening until it was too dark for observations to be made; in contrast, during dry season months animals rarely moved until two or three hours after sunrise, and were usually settled for the night about three hours before sunset. Thus light levels did not play a crucial role in determining the onset and cessation of activity in the groups studied, although it may have been a minor contributing factor.

Vegetation. The pattern of group dispersion varied strikingly between the two study areas. No causal chain of well-defined ecological factors was pin-pointed to account for this variation. However, out of a number of possible explanations the following hypothesis, based on estimated differences in the distribution, size and availability of food sources, is put forward as being the most probable on current evidence. In the north, it is argued, groups required their total home-range in the course of a whole year. Their diet contained a wide range of foods which were in many cases distributed in small, scattered resource units that

occurred rarely in the forest and were often only seasonally available. As these different foods became available, so the area over which animals had to range shifted. Thus, at any one time the most crucial dietary items available within the group's home-range met the group's requirements, while the total food available was likely to be in excess of its requirements. This permitted extensive overlap between the ranges of neighbouring groups. It is likely that it was more efficient for groups to range regularly throughout their total home-range rather than through a smaller, seasonally shifting area: the former, wider ranging pattern allowed them regularly to "monitor" the presence or absence of scattered seasonally available food sources. In contrast, food probably did become a limiting factor for the southern groups towards the end of the dry season, because of the effect on the vegetation of the extreme aridity at that time. It is suggested that during these critical periods, the food available within each home-range could support only one group without the forest's carrying capacity being exceeded. The round-the-year territoriality found in the south may have been an adaptive response to this minimum foraging area requirement which operated at times of greatly reduced food availability.

In the dry season in both study areas, animals moved short distances each day and fed for short periods on a wide variety of food species. In the wet season, they moved further each day, and fed for longer periods on fewer species. The possible contributing role of fluctuations in temperature to this seasonal variation has already been referred to. Changes in the availability and distribution of food may also have played a part in determining this seasonal variation. It was estimated that there was a higher density of vegetation in the northern study area, and it is likely that this relfected higher primary productivity in that area. It is also probable that in both study areas productivity was greater in the

wet season than in the dry. Reduced productivity in the dry season may have been associated with a decrease in the availability of food although it should be emphasized that there is no necessary correlation between overall productivity and the availability of food for any one animal species. If such a decrease is assumed, it can be postulated that this caused a reduction in the amount of time animals spent feeding. This would have led to a net reduction of available energy and hence a decrease in the length of day ranges. However, the underlying assumption cannot be demonstrated and may well be invalid.

An alternative hypothesis, for which there is at least some evidence is that seasonal changes in ranging patterns may have been determined in part by changes in the distribution and availability of certain foods and associated changes in the degree of selectivity exercised by the animals. The vegetational analysis indicated that many tree species in both forests tended to be widely scattered. Further, during both seasons, over 50% of the species eaten by the study groups were quite rarely occurring in both forests. In the wet season, animals mainly ate the fruit of a few species. In order to seek out adequate supplies of these few species they had to range widely each day. In the dry season little or no fruit was available and animals were much less selective in their choice of food. They ate the leaves of many species and thus did not have to travel far each day in order to find adequate, if unappetizing, food. Thus, it is argued, these closely related changes in food availability and selectivity effectively altered the distribution of the main components of each group's diet and, hence, the group's ranging pattern.

Conclusions

The study provided enough detailed information on Propithecus verreauxi to indicate that this species responds to regional and seasonal

variation with behavioural adaptations. It also showed that the social organization of P. verreauxi cannot be neatly pigeon-holed with that of other so-called "folivorous-frugivorous" primates such as Colobus badius or Alouatta palliata. However, I believe that perhaps the most significant results lay in the fact that it indicated the potential value of an analytically approach to primate field studies.

Current classifications of primate societies on the basis of gross ecological parameters are of low predictive value: the social organization of a given species can rarely be predicted on the basis of its being a "forest-dwelling," "leaf-eater." In this study, an attempt was made to show that by the use of a more rigorous, analytical methodology, certain correlations can meaningfully be made between social organization and ecological parameters. These may increase our understanding of the inter-specific variation observed in the social organization of primate species.

Among the primates, social organization is the result of an extremely complex interaction of parameters including the dietary prerequisites of the species, the size, abundance, distribution and seasonality of food resources (including water), the climatic parameters of the environment and animals' physiological and behavioural capacity to respond to these parameters, predation pressures, the length of infant dependency, and the overall density of population. It is acknowledged that in the present study, a relatively superficial investigation of only a few of these paramaters was carried out, and many further methodological refinements remain to be made. To take but one example, the estimation of home-range size is considered to have been inadequate and efforts will be made to evolve a more accurate, three-dimensional means of measurement in future work. Many of the conclusions reached were tentative, in that they may be misinterpretations of poorly substantiated patterns of activity of animals or distribution of foods. In a non-experimental field study,

causation can only be inferred from associations demonstrated between aspects of social organization and features of the environment. Such inferences may often be fallacious.

However, despite the shortcomings referred to above, I believe that the question posed, "How is social organization influenced by environment?" is valid, and that a detailed quantitative approach can provide some answers. It is unlikely that we shall ever be able to predict social organization from a spectrum of known ecological variables with 100% certainty and, in view of the complexity of factors involved, equally unlikely that a simple system of classification will emerge. However, this essentially multivariate approach can elucidate both the mechanisms by which animals exploit and are exploited by their environment and the corollaries of this exploitation.

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